THE

NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL

EDITED BY

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SHERARDIAN PROFESSOR OF BOTANY
IN THE UNIVERSITY OF OXFORD

VOLUME XXIX

PAGES vi AND 360

WITH TWO PLATES AND NUMEROUS FIGURES
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THE

NEW PHYTOLOGIST

FURTHER STUDIES ON THE HETEROKONTAE:

SOME HETEROKONTAE OF NEW ENGLAND, U.S.A.

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(With 4 figures in the text)

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INTRODUCTION

THE present study was undertaken by the author as holder of the
Seessel Fellowship at Yale University, U.S.A., during the year
1928–1929. The intention to continue the study in America for a

second year had to be abandoned unexpectedly. Nevertheless, it has seemed advisable to publish the present paper as the study is to some extent a local one, although the work is necessarily incomplete. It may serve a useful purpose as a record of the species found. Meanwhile further studies on the genera described below, as well as others, are being continued in England.

I wish to record my gratitude to various members of the Department of Botany of Yale University. To Dr G. S. Nicholls the Head of the Department, and to Dr Alexander W. Evans, former Head of the Department, I am indebted for their kindness in putting the resources of the Department at my disposal, and for much assistance during the progress of the work. To Dr H. Castle my thanks are due for his invaluable help in the collection of material for study, while Dr Carl Deuber was kind enough to advise me regarding the chlorophyll tests described at the end of this paper. To Mr and Mrs Hutchinson of the Department of Zoology of Yale University, I owe my thanks for their assistance in obtaining material from the fresh-water plankton of some local ponds, also for supplying me with preserved material of *Botryococcus* from South Africa. In addition, I have had the benefit of valuable advice from Dr W. Randolph Taylor of Philadelphia, Dr Gilbert M. Smith of Berkeley University, California, and also from Professor F. E. Fritsch of London.

The method employed was to make frequent collections of fresh material from different localities during the months of October and November 1928. Little material was obtained during the winter months, and further collections were made from early April to the end of July both from the same and from other localities. The fresh material was carefully examined, and when members of the Heterokontae were observed, they were isolated as far as possible and grown under conditions of pure culture following the method described by Chodat in *Étude critique sur le Polymorphisme des Algues*.

This process naturally involved a long delay before the alga could be studied in complete isolation. Meanwhile the attempt was made to keep specimens of the fresh Heterokontean material under conditions more closely approximate to those of nature. Fresh collections were placed in a very weak culture solution, Detmer's solution 0·1 per cent. and Moore's solution[1] 0·1 per cent. being usually employed.

[1] Composition of Moore's Solution.

Ammonium nitrate	0·5 grm.	Calcium chloride	0·1 grm.
Monobasic potassium phosphate	0·2 grm.	Magnesium sulphate	0·2 grm.
Iron sulphate	Trace	Water	1000 c.c.

These samples were kept at a fairly low temperature in a glass cupboard which was fixed to the window in a cool room. The temperature was regulated by opening and closing the window. The aspect of the window allowed direct sunshine to reach the algae for an hour or two daily. Many of the specimens were thus kept alive during the whole of the winter. Further culture solution was added from time to time to replace that lost by evaporation. During this period observations were made on the material and these afforded a useful check on those made on the algae which were grown under conditions of pure culture. While I am more than ever convinced of the value—perhaps one should say the necessity—of the observation of the life histories of algae over prolonged periods under conditions of pure culture, I believe it to be highly desirable to compare constantly the behaviour of the algae under circumstances more closely approximating to the natural conditions. Such a study will be particularly useful in those cases where the organism exhibits a tendency to polymorphism under the unnatural conditions. A further precaution was taken by employing varied media for the pure cultures—liquid and solid. The media chiefly used were as follows:

Liquid

(a) Detmer's solution, $\frac{1}{8}$ and $\frac{1}{10}$.   (b) Moore's solution, $\frac{1}{8}$ and $\frac{1}{10}$.

On the whole better results were obtained from (b) than from (a).

Solid

(a) Agar, 1 or 2 per cent.   (b) Agar, 1 or 2 per cent.
Detmer's solution, $\frac{1}{8}$ or $\frac{1}{4}$.   Moore's solution, $\frac{1}{8}$ or $\frac{1}{4}$.

(c) Agar, 1 per cent.   (d) Agar, 1 per cent.
Peptone, 0·16 per cent.   Peptone, 0·16 per cent.
Detmer's solution, $\frac{1}{8}$ or $\frac{1}{4}$.   Moore's solution, $\frac{1}{8}$ or $\frac{1}{4}$.

No sugar-containing cultures were used, except in the case of *Ophiocytium* (see p. 16). In order to transfer the alga to the medium the usual method was followed, viz. repeated washings were made with sterile water followed by vigorous shaking (except in case of filamentous forms). In addition the material was often washed in very dilute Upsulum solution in order to reduce the risk of infection by bacteria.

With regard to the localities from which the algae were collected, no attempt was made to cover a very large area. Collections were made during the autumn of 1928 and spring 1929 from the neighbourhood of New Haven, Connecticut, pools and streams being very

abundant even within a radius of a few miles. The greatest distance from New Haven at which material was collected was approximately eight miles. A considerable amount, however, was gathered at much shorter distances than this. The locality is quite a favourable one for the study of algae.

Further collections were made during the summer of 1929 from the neighbourhood of Wood's Hole, Massachusetts, where the study was continued at the Marine Biological Laboratory. Both the mainland and the neighbouring islands, with their numerous pools and ponds, afford a fine opportunity for the collection and study of algae, including fresh-water, brackish, and marine species. In the case of *Botryococcus* I have had the advantage of preserved material from the plankton of certain South African lakes, in addition to the fresh material from the localities mentioned above.

The present work tends to emphasise the fact that in the study of algae due attention should be paid to the cytological and chemical as well as to the morphological and physiological characters. For instance, the presence of silica in the wall is a feature which is quite constant when it occurs, and is a reliable specific character. Similarly with the presence of a large proportion of xanthophyll in the chlorophyll; the occurrence of oil or fat in the cytoplasm, etc.

The close parallelism of the Heterokontae to the Isokontean series raises a number of undetermined questions. It is usually regarded as representing the expression of a similar evolutionary tendency, assuming the two groups to have been derived from different Flagellate ancestors. On the other hand, it may point to a closer relationship, on the theory that the Heterokontae have arisen by divergence from the green series. In any case, such striking likenesses as, for example, that of *Botrydium granulatum* and *Protosiphon*; *Characiopsis* and *Characium*; *Heterococcus* and *Protococcus*; to mention only a few, should be carefully borne in mind when deciding that the two groups are entirely independent. In the present state of our knowledge, perhaps the question of parallelism should not be pressed too closely. It should always be remembered that, in spite of a close superficial resemblance, in no member of this series has reproduction by sexual methods—neither isogamy nor heterogamy—been definitely established. Finally there is the question of the complete absence of elaboration of the chloroplast, which is so marked a feature in contrast with the Isokontean series. Small disc-like chloroplasts are but rarely found in the green algae, notable exceptions being *Eremosphaera* and *Vaucheria*. Further, though the

filament and the siphon are both represented in the group, neither can be regarded as the typical form. They are indeed almost the exception—so far but one siphonaceous and two (or at most three) filamentous genera having been recorded. The emphasis in the Heterokontae seems to be towards the development of the unicell and the colony. Whether this feature has any relation to the lack of sexuality, it is impossible to decide. At any rate, as the work on the Heterokontae continues, it confirms the view that the group is a natural one, whether it arose directly from Flagellates or by reduction and simplification of various Chlorophyceae. On the whole the former possibility seems the more likely one.

The scheme I have followed in classifying the algae is that of Pascher in *Die Süsswasserflora Deutschlands, Österreichs und der Schweiz*, 1925, which at the present stage of our knowledge remains the most satisfactory that has been advanced.

STIPITOCOCCUS URCEOLATUS W. AND G. S. WEST

Stipitococcus urceolatus was found quite commonly in various pools in the neighbourhood of New Haven, Connecticut, also in the vicinity of Wood's Hole, Mass. This alga is usually gregarious, though occasionally solitary cells occur. It was found most frequently attached to filaments of *Mougeotia*, for which alga *Stipitococcus* appears to have a decided preference (Fig. 1 A). Though filaments of *Spirogyra* and *Zygnema* often occurred abundantly in the same sample they were usually quite destitute of the epiphyte. However, in one instance *Stipitococcus* was found on a filament of *Zygnema* in material which had been kept for some time in the laboratory. It has also been observed growing quite healthily upon decayed *Mougeotia* filaments. Occasionally it is found growing on filaments of *Oedogonium*.

Stipitococcus urceolatus is a small fragile unicellular epiphyte which is very pale green in colour. Often it appears almost colourless. However, in a strong light and with fairly high magnification it appears distinctly green. In shape the cell is rounded or oval and has one end prolonged into a delicate stalk which ends in a minute expansion (Fig. 1 B). This is not easily seen unless it is stained. By means of this tiny disc the alga is attached to the filament on which it is growing. The other end is pointed or blunt; it may also be expanded, and frequently this portion appears to break open rather irregularly, sometimes forming a sort of tuft, which gives the cell the appearance of a tiny thistle (Fig. 1 B). In the natural state it is

often possible to discern only the two ends of the torn membrane, and these have the appearance of two fine processes which grow from the more swollen portions of the cell. On staining with safranin, however, the intermediate portion of the delicate membrane is clearly seen and this usually has an uneven edge. The horn-like projections are often equal in length to the more swollen parts of the cell; sometimes however they may be shorter or longer than this. Usually among the group of *Stipitococcus* cells some appear to be quite devoid of protoplasmic contents.

The cell wall, which stands somewhat apart from the rest of the cell, is very delicate but well defined when stained with aqueous safranin. Congo red colours it distinctly, including that part of the wall which forms the tuft alluded to above. Methylene blue caused practically no change. The application of Schultze's solution caused the cell contents to stand out very clearly but resulted in no distinct coloration of the wall. It appears therefore that the wall is composed of cellulose with little or no pectic material (the test with Schultze's solution being unreliable when a negative result is obtained).

Each cell seems to be furnished with a single chloroplast which appears exceedingly pale, hardly a trace of green or yellow-green colour being visible even in the natural state. On warming with strong hydrochloric acid the chloroplast became aggregated and appeared distinctly blue-green, suggesting the presence of xanthophyll. A pale reddish spot was visible in many of the cells.

The contents of the cells are very granular, the granules being minute and blackish in appearance. Iodine solution caused these granules to become very evident as they are stained brownish red. No starch was observed nor was a pyrenoid present. Schultze's solution revealed the cell contents very clearly as they assumed a greenish colour, but no starch was visible. A single nucleus was present in the cells, which is brought into evidence by staining with safranin or gentian violet (Fig. 1 B, C).

Reproduction

Asexual reproduction is brought about by the formation of zoospores, which takes place in the following manner: Through the opening in the cell wall (at the end opposite to the stalk) already referred to, long vibratile filaments extend, causing a diminution of cell substance within the cell itself, this often results in an apparently empty space at the opposite end. These filaments are evidently

protoplasmic and resemble the rhizopodial filaments of some of the members of the Chrysophyceae (Fig. 1 D, E). They are extremely sensitive to reagents. The application of iodine solution or Congo
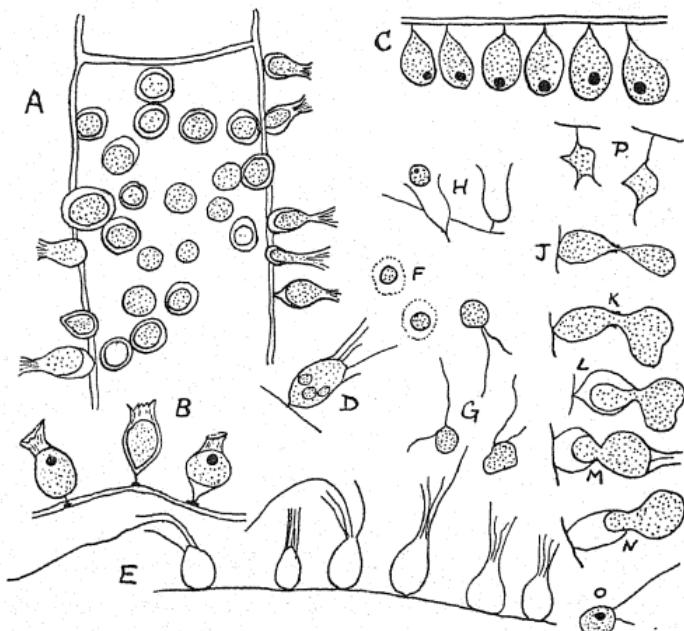
Fig. 1. *Stipitococcus urceolatus.*

A. *Stipitococcus urceolatus* growing on filament of *Mougeotia.* ×900.
B. Individual cells showing minute disc of attachment, also open ends, and nuclei. ×900.
C. Series of cells stained with safranin to show nuclei. ×900.
D. Single cell containing 3 zoospores. Vibratile filaments shown. ×900.
E. Series of cells showing vibratile filaments. ×675.
F. Two zoospores with "sheath" having just been liberated. ×675.
G. Three zoospores provided with cilia. ×900.
H. Two empty cells having discharged their zoospores. ×900.
J–O. The same cell drawn at intervals of about 2–3 minutes showing formation of a zoospore from the whole of the contents. M shows two or three fine filaments which afterwards disappeared. O shows the rounding off of the contents to form a zoospore which has two unequal cilia. ×675.
P. Two zoospores becoming attached to *Mougeotia* filaments, and making amoeboid movements. ×500.

red forces them to draw together in the form of a small brush instead of diverging as before. They are often seen to be in a state of rapid vibration. The number of filaments is usually but not invariably four. They have the appearance of excessively fine bristles of uneven

length, and are easily overlooked owing to their extreme delicacy. Frequently it is impossible to see them clearly until a reagent, e.g. iodine, has been applied. Often the bristles are very long, being as much as four to five times the length of the cell (excluding the stalk)[1].

From time to time a small almost colourless zoospore emerges from the cell. It appears to be passed slowly along one of the protoplasmic filaments to the tip and it then escapes, moving at first very slowly and tentatively.

At this stage it is surrounded by a colourless transparent vesicle which soon disappears (Fig. 1 F). After a few minutes of slow somewhat amoeboid movement the zoospore suddenly moves very rapidly and swims away. This is due to the acquirement of a pair of cilia which in some cases were clearly visible without the use of reagents. They are distinctly unequal in length, the long one being two to four times the diameter of the zoospore. The short one is from one-third to one-half the length of the long one. The cilia are very clearly seen on killing the zoospore with aqueous solution and afterwards staining with weak aqueous safranin. By this means both cilia are seen with perfect clearness (Fig. 1 G).

The zoospore at first appears to be filled with granular protoplasm and rather greenish-grey in colour. Some of the granules are very bright, others appear black. Occasionally a pale red spot is seen within the protoplasm. The zoospore increases in size slightly, and as it moves it becomes rounded or narrowly pear-shaped. The longer cilium is usually directed backwards during the movement. Several zoospores are formed within the cells, two or three being the usual number seen (it is probable that more than these are commonly formed) (Fig. 1 D).

Sometimes the greater part of the contents emerges through the opened cell wall, no vibratile filaments being formed. The movement is at first slow, and on emerging the mass of protoplasm becomes amoeboid. Fig. 1 J–O represent a series of stages in formation of the zoospore by this method. They show the same cell at intervals of a few minutes. The final stage (O) shows the mass which is no

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[1] I have found no evidence that the filaments by their movements serve to waft minute particles to the cell beneath as is the case in some of the Chrysophyceae. Though little chlorophyll is present *Stipitococcus* appears to be holophytic in its method of nourishment unless there is anything in the nature of a parasitic relationship between the alga and its host, a suggestion which has no evidence to support it beyond the very slight amount of chlorophyll present and consequent paleness of the cells.

longer amoeboid but has acquired a pair of unequal cilia, soon after which it swims away.

After moving about for a time the zoospore becomes quiescent, and it seems that several small pale greenish processes are put out from the cell, radiating in the form of a star (Fig. 1 P). These processes are somewhat amoeboid in character and their movement, though very slow and sluggish, is quite definite. It is quite probable that by this means the young *Stipitococcus* cell is able to anchor itself to a filament. The contents are precisely similar in appearance to those of a mature cell. There was no evidence to support the suggestion of W. and G. S. West[1] that the stalk of *Stipitococcus* is probably formed from a cilium of the zoospore.

No cysts have been observed in the genus. The manner in which the alga passes the winter is completely unknown.

Cultures

All attempts to cultivate *Stipitococcus* on agar or in sterile culture solutions proved a failure, though many attempts were made, using very varied media with *Zygnema* filaments which were rich in the epiphyte. All the observations have therefore been made on fresh material. However, it was often found possible to obtain a good crop of zoospores even in five to six hours in a hanging drop culture using 10 per cent. Moore's solution. No other algae were detected in the material used except *Mougeotia*, *Spondylosium* and *Zygnema*. Small zoospores were frequently found settling on filaments of *Mougeotia* and empty *Stipitococcus* cells were frequent.

Systematic position

Stipitococcus urceolatus was first described in 1901 by W. and G. S. West[2] who referred it to the sub-family Characieae (near Characium) in the family Palmellaceae of the Protococcoidae. Since then, reference has been made to it by other investigators, as for example Pascher[3], who gives a short description of the alga and suggests that possibly its true place is not among the Heterokontae but that it should be regarded perhaps as a rhizopodial Chrysomonad.

The pale chloroplast, the habit of forming rhizopodia and the amoeboid movement of the zoospores when first formed lend support to this view. In spite of these resemblances of *Stipitococcus* to many

[1] *Alga Flora of Yorkshire*, 1901, p. 127.
[2] *Ibid.*
[3] *Süsswasserflora*, Heft 11, S. 27.

of the Chrysomonadineae, however, it appears to the writer that the position of the alga as a member of the Heterokontae is a perfectly natural one. Temporary amoeboid stages are known to occur in the zoospores of several members of the Isokontae, as well as in many Chrysophyceae and Dinophyceae as Fritsch[1] points out. They are recorded by Pascher also for *Bumilleria sicula*—an established member of the Heterokontae. Besides, the Heterokontean alga *Chloramoeba* is typically amoeboid. Hence it would appear inappropriate to withdraw *Stipitococcus* from the Heterokontae on this account. The same applies to the formation of rhizopodia, a character which is particularly marked in many of the Chrysomonadineae. It should be noted that *Heterochloris*, an accepted member of the Heterokontae, also exhibits this habit.

Further, the absence of cysts as far as is known and of golden brown chromatophores (though, according to Pascher, in a few cases members of the Chrysomonadineae have blue-green chloroplasts) as well as of vacuoles, contractile or otherwise, differentiate this alga from the Chrysomonadineae. Certainly the presence of a relatively large amount of xanthophyll in the chloroplasts, the complete absence of starch as assimilation product, and the unequal length of the cilia of the zoospores bring it into line with the other members of the Heterokontae, though it is certainly a lowly member of the series. Its appropriate place would then be as a member of the group Rhizochloridales not far removed from the Heterochloridales, which includes the rhizopodial *Heterochloris* and the amoeboid *Chloramoeba*. All these may be regarded as lowly members of the series having distinct affinities with the group Chrysomonadineae.

BOTRYDIOPSIS MINOR CHOD.

Botrydiopsis minor was found in two localities, viz. (1) near Falmouth, Mass., (2) on the island of Cuttyhunk, Cape Cod, Mass. The diameter of the cells was $16 \cdot 2\mu$. The cell contents and general features agreed with the author's previous description of this species[2]. Autospores were frequent, but no zoospores were observed.

CHLOROBOTRYS STELLATA CHOD.

This alga was found very abundantly attached to stones in the bed of a small stream which ran through a railway cutting near New Haven, Connecticut. It was also found in the following localities:

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[1] *Biological Reviews*, Cambridge, **4**, No. 2, 1929.
[2] *Études sur les Hétérokontes*, p. 20.

(1) Golf Links, New Haven. (2) On greenhouse pots, Yale University. (3) On the island of Nonamessett, near Wood's Hole, Mass. In specimens from each of these localities very many of the cells exhibited the characteristic stellate form, as described in a former study[1] (Fig. 2 A–D). As I have previously suggested, the assumption of the stellate form is probably due to some physical condition of
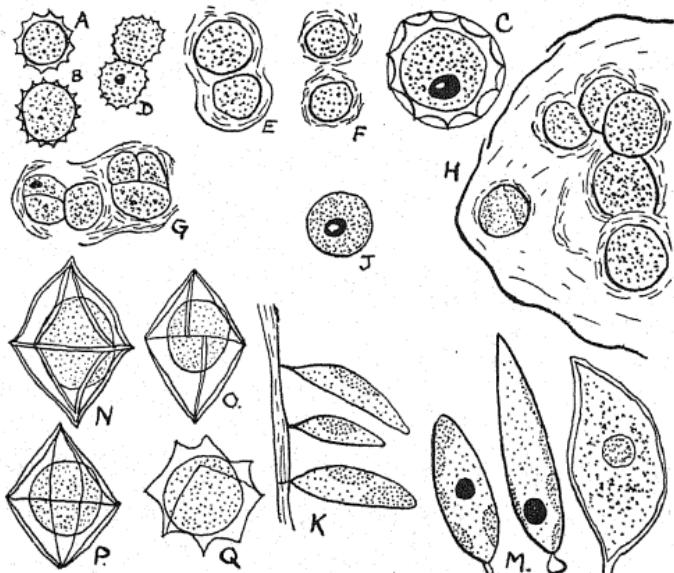
Fig. 2. A–H, *Chlorobotrys stellata.* K–M, *Characiopsis.*
N–Q, *Bernardinella bipyramidata.*

A, B, C. *C. stellata* (fresh material) separate cells showing stellate walls. ×900.
D. Showing cell division (fresh material). ×500.
E, F, G, H. Cells showing membranes and "false coenobia." ×900.
J. Cell showing simple wall. ×500.
K. *Characiopsis acuta* on *Rhizoclonium* filament. ×500.
M. *Characiopsis Heeringiana* (3 cells). ×900.
N–Q. *Bernardinella bipyramidata.* Q, view from apex. ×1000.

the cell wall. The cells adhere in masses or "false coenobia" (Fig. 2 G, H) which are held together by pectin, and the outer layers of the walls are frequently cast off (Fig. 2 F). The cells are very firm and resistent owing to the presence of silica in the walls.

The inner structure of the cells resembled that of the previously described specimens in respect of the chloroplasts with their rather

[1] *Études sur les Hétérokontes*, 1927.

indistinct outlines; the presence of a large oil-spot (Fig. 2 C, J); the small granules, and the occasional occurrence of a red spot. In all points of structure this alga resembled the one alluded to.

No "cysts," such as are said to occur in *Chlorobotrys regularis* have been observed either in the American or the Genevan material. They appear to be completely absent from this species.

Cultures

Chlorobotrys stellata lends itself very readily to culture—both in solid and liquid media. On agar it formed a dark olive-green patch, more or less circular at first, but eventually becoming raised in the middle. Stellate walls were seldom seen under cultural conditions, most of the cells having smooth walls. Fritsch[1] remarks that *Chlorobotrys stellata* has hitherto been known only in cultures. The presence of stellate forms in material obtained from these four different localities establishes beyond doubt the existence of this species, which differs from *C. regularis* not only in the presence of the stellate wall, but in the complete lack of regularity in the arrangement of the cells. Further I cannot agree with Fritsch when he says that "the assignation of this alga to the genus *Chlorobotrys* appears doubtful." Apart from the question of the zoospores, which up to the present have not been observed in *C. regularis* and but rarely in *C. stellata*, the algae agree in general characters; the regularity of the colony in *C. regularis* being the most noticeable difference between the two species. The silicified walls, the chloroplasts and the cytoplasmic contents are similar in both.

The most outstanding difference appears to be the occurrence of bivalved silicified "cysts" which are recorded by Bohlin for *C. regularis*. However, since it is not certain whether the "cyst" belongs to *C. regularis* or not, it is well not to rely on this character too closely.

Zoospores

No zoospores were observed in any of the cultures of *C. stellata*. However, in fresh material containing as far as could be ascertained no other alga but *Oscillatoria*, numerous zoospores having unequal cilia were distinctly seen. Each had a single chloroplast and a faint red spot. They agreed in character with those already described[2]. The long cilium and occasionally the shorter one were seen distinctly without the use of reagents. The former was directed backwards

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[1] *British Freshwater Algae*, West and Fritsch, p. 307, 1927.
[2] *Études sur les Hétérokontes*, p. 14.

during the movement, the short cilium pointing in the direction of the movement.

CHLOROBOTRYS REGULARIS WEST, BOHLIN

This species was obtained in large quantity from Falmouth, Mass. The regular colonies were composed of two, four, or more cells which were arranged in pairs united by transparent pectic material. The cell walls contained silica and in all respects agreed with the descriptions of Bohlin and others except that no "cysts" were observed.

[BERNARDINELLA BIPYRAMIDATA CHOD.]

This interesting little alga was first observed by Chodat[1] from the Grand St Bernard region of Switzerland. As far as I have been able to ascertain no other record of the alga has been made hitherto for America. It was found in small quantities in a large pool on the island of Cuttyhunk, Cape Cod, Mass., and it is interesting to note that the pool was at one time used for washing sheep which came from Europe. The alga might conceivably have survived transportation over such a long distance owing to its characteristic hard shell. The cell exhibited the bipyramidal form with a number of longitudinal ribs and a prominent equator (Fig. 2 N–P). The wall was pale brown in colour, the deep green spherical protoplast being clearly visible within. Seen from the apex the cell appeared stellate in outline (Fig. 2 Q). The dimensions of the complete cell were: length, $23·8\mu$; breadth, $14·9\mu$; diameter of the globular mass within, $10–11\mu$. It was impossible to isolate or to cultivate the alga owing to its appearing in such small quantity. No form of reproduction was observed.

Systematic position and affinities

As long as nothing was known regarding the reproduction of *Bernardinella* it was impossible to assign it with any degree of certainty to any definite group. Chodat[2] suggested that it was a Flagellate probably belonging to the Lepochromadaceae. Pascher[3], who gives a description of the alga based on the record of Chodat already alluded to, adds that we do not know whether it is a vegetative stage or a resting stage of an alga. He further calls attention to the fact that G. S. West has described and figured from Ceylon a similar green alga *Desmatractum plicatum* which possibly represents

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[1] Chodat, "Algues de la région du Grand St Bernard," *Bull. de la Société Botanique de Genève*, 1920.
[2] *Ibid.*   [3] *Süsswasserflora*, Heft 11.

the same organism. West placed this provisionally in the Proto-
coccales. This alga evidently bears a distinct resemblance to *Ber-
nardinella* though it is described as being considerably smaller, its
dimensions being: length, 16–17μ; breadth, 6·5–7μ. It is probable
that the measurements are taken from a young individual[1].

The next mention of *Bernardinella* is that by G. Deflandre[2] who
records it from France. Finally in 1928 A. A. Korshikov[3] has given
more details of the structure and reproduction of the alga. He states
that starch is present, and he has observed and figured a method of
reproduction by cell division, eight daughter cells being formed
within the greatly distended envelope of the mother cell. Each is
provided with a colourless outer membrane of the typical bipyra-
midal form. Hence it seems unlikely that they are zoospores.
Korshikov considers that these are not zoospores because of the
absence of a stigma. Yet in many of the Heterokontae this character
is lacking in the zoospore. Further, he asserts that one or two con-
tractile vacuoles were clearly present in each young protoplast but
that these disappeared immediately before an inner membrane was
formed round the protoplast. He regards the "daughter cells" as
autospores which he suggests are reduced zoospores. The contractile
vacuoles are a zoosporic character, though the bipyramidal wall
emphasises the autosporic nature of these cells. Korshikov thinks
that there may be reproductive cells which are intermediate in
character between zoospores and autospores and refers to *Glauco-
cystis nostochinearum* in which similar cells are found. It would
appear therefore that further observation of the "autospore" of
Bernardinella is necessary before we can be quite certain as to the
correct systematic position of the alga. At any rate Korshikov has
shown clearly that this alga is not a resting stage as Pascher imagined
but a normal vegetative condition. As starch was found *Bernardinella*
is probably not a member of the Heterokontae, as had previously
been held. In the light of the interesting contribution of Korshikov
it seems appropriate to withdraw it from that group and to place it
provisionally among the Protococcales as he suggests[4].

[1] Pascher, *Süsswasserflora*, Heft 5, S. 55, 1915.
[2] "Sur une algue rare *Bernardinella pyramidata* Chod. nouvelle pour la flore
française," *Archives de Botanique de René Viguier*, Tome I, Bulletin mensuel,
no. II, Nov. 1927.
[3] "Notes on some new or little-known Protococcales," *Archiv für Protisten-
kunde*, 62, Heft 2–3, 1928.
[4] For the sketches of this alga I am indebted to Miss H. Croasdale of
Philadelphia.

CHARACIOPSIS BORZI

Five species of *Characiopsis* were met with[1]. The following from the neighbourhood of Wood's Hole, Mass.[2]:

Characiopsis pyriformis (*Characium pyriforme*, A. Braun).

C. longipes Borzi.

C. minor Pascher.

In the salt marshes near New Haven there occurred the following species:

C. acuta Borzi (Fig. 2 K).

C. heeringiana Pascher (Fig. 2 M).

C. heeringiana was examined in some detail. It was found to agree in cytological characters with the description given for *C. ovalis*[3]. One nucleus is present in the cell. This species was found to assume a considerable variety of forms as shown in the figures (Fig. 2 M). No zoospores were observed in any of these species.

OPHIOCYTIUM NAEG.

The following species of *Ophiocytium* were found:

Ophiocytium arbuscula Rabenhorst from several localities in the neighbourhood of New Haven, Conn.

O. cochleare A. Braun from the islands of Pasque and Nonamessett, Cape Cod, Mass.

O. majus Nageli from the island of Cuttyhunk, Cape Cod, Mass.

O. capitatum Wolle from the island of Nonamessett, Mass.

O. arbuscula was usually found attached to filaments of *Mougeotia*. In some of the cells six zoospores were distinctly observed within a cell (Fig. 4 B). These appear to escape from the upper end of the cell, the "lid" having probably become previously detached (Fig. 4 C). The cilia of the zoospores were not observed.

A curious case was observed in which the curved *Ophiocytium* cell (*O. arbuscula*) appeared to have been transformed into separate cells. These formed a single rank for part of the length, the remainder constituting a double series, the whole being roughly U-shaped (Fig. 4 E). The individual cells had the firm walls and the rather pale contents characteristic of the species. I have observed only one example of such a filament, but, if it is confirmed, we have a clear

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[1] The species are named according to Pascher (*Süsswasserflora*). In the present state of our knowledge these should be regarded as somewhat provisional. A thorough revision of this genus is necessary.

[2] *C. pileata* (Copeland) has been recorded from this district by Lewis and Taylor. *Rhodora*, Oct. 1928.

[3] Poulton, *Études sur les Hétérokontes*, p. 32.

case of the formation of akinetes. As far as I am aware these have not previously been recorded for *Ophiocytium*.

Cultures

Pure cultures of *O. arbuscula* were obtained on several media, viz.

Agar, 1 per cent.
Peptone, 0·15 per cent.
Dextrose, 1 per cent.
Moore's solution, $\frac{1}{5}$.

Agar, 1 per cent.
Peptone, 0·1 per cent.
Moore's solution, $\frac{1}{5}$.

Agar, 1 per cent.
Moore's solution, $\frac{1}{10}$.

Agar, 1 per cent.
Moore's solution, $\frac{1}{5}$.

On all these media the alga appeared to thrive, but growth was in all cases exceedingly slow. For example, after about six months the dark green patch covered an area of no more than about 25 sq. mm. Many of the cells were circular in outline, many were elongated and some became curved. The arm walls was noticeable and a slight swelling of the wall took place on heating with caustic potash solution. No reproduction was observed under conditions of culture.

BOTRYOCOCCUS BRAUNII KÜTZING

Fresh material of this alga was obtained from pools on the island of Cottyhunk, Cape Cod, Mass., also from the plankton of the lakes of Mount Carmel, Conn. Preserved material was examined from the plankton of certain South African lakes, viz. Malati Lake, near Masseyeri, South Tchopiland, Portuguese East Africa; also from a dam near Trichard, Bethal District, Transvaal, South Africa.

The colonies appear as opaque amorphous masses, often brick-red in colour. When examined against a dark background, masses which ordinarily seem to be black appear distinctly as pale or bright yellow or light green clusters. On squeezing one of these masses some of the individual cells emerge, when they are seen to have a firm cell wall and to vary considerably in shape—some being almost globular, others pear-shaped, kidney-shaped or elliptical, while others are quite irregular in outline (Fig. 3 A). The dimensions of the cells are: length, 6–10μ; breadth, 3–5μ.

Methylene blue stains the cell wall faintly blue, showing that a considerable amount of pectic material is present. In some cases there is some indication of the presence of a short stalk at one end, as though the cells are attached. However, this feature was not observed in all cases.

The cell contents are granular and at times a distinct colourless spot is discernible. Sometimes two of these are present. Individual chloroplasts are not visible, though the contents as a whole appear green. It seems probable that only one chloroplast is present in each cell[1]. Iodine solution stains the contents brownish, the small granules assuming a darker brown colour. No starch or pyrenoid was observed. No separate chloroplasts are seen after staining. A single nucleus is present in each cell, as shown by staining with safranin (Fig. 3 A).
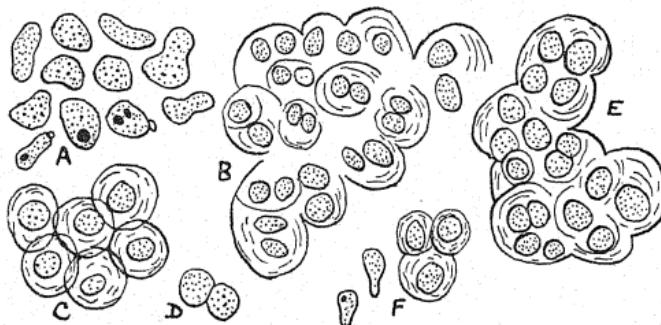
Fig. 3. A–E, *Botryococcus braunii*. F, *Botryococcus protuberans*.
A. Group showing separate cells of various shapes with granular contents. Two show a minute appendage (? stalk). ×900.
B. Group of cells within the membrane after exposure to xylol. Cell division indicated. ×500.
C. Group of cells after the red colour has been removed by acetone, and subsequently treated with methylene blue. ×800.
D. Two escaped cells showing vegetative division. ×800.
E. Part of colony, treated as C, showing cell division and lamellated membranes. ×800.
F. *B. protuberans* showing single cells, and three cells from the colony showing thick lamellated membranes around each cell. ×500.

On heating alternately with strong sulphuric and strong hydrochloric acids, not only do the masses of cells keep their characteristic form, though they lose the red colour completely, but individual cells also retain their outline as far as can be seen from those that can be squeezed out from the colonies. The cell walls are therefore very resistant, probably owing to the presence of silica. A very large number of cells remained intact even after a second treatment with the acids.

[1] I have been unable to determine the shape of the chloroplast with certainty. Chodat (*Algues vertes de la Suisse*, p. 20) states that *B. braunii* has one chloroplast in each cell, which is bell-shaped and lobed on the edges.

The cells appear to be grouped together in separate, more or less spherical masses. This is shown after the red oily material has been largely removed.

The red oily substance, which obscures the structure of the colonies of *Botryococcus* and has hitherto militated against our knowledge of the alga, was subjected to treatment by various reagents. Carbon disulphide did not immediately dissolve it. At first there was no apparent change, but drops of oil gradually appeared in the field and became abundant. After exposure to the reagent for half an hour the mass became distinctly paler and the green colour of the cells could be clearly seen. After a longer period the red colour completely disappeared.

Xylol caused no immediate change, not even after a period of fifteen minutes. After half an hour, however, the membrane appeared distinctly paler, and at the end of an hour the red colour had so far disappeared that the individual green cells could be clearly seen through the membrane, which had become pale on the edges (Fig. 3 B). After five hours scarcely a trace of the red colour was visible. Globules of oil were very abundant near the surface of the colony, and on the application of pressure to the coverslip a further quantity could be squeezed out.

After exposure to acetone for five hours the red colour had almost disappeared on the periphery of the mass, though it was still visible in the interior. A similar result was obtained with benzene. Alcohol (95 per cent.) gave a precisely similar result. Strong potash caused no apparent change, but on warming many oil-drops appeared in the field. When warmed with strong sulphuric acid the red colour gradually disappeared and the mass became blue-green or brown-green.

The above tests show conclusively that the red material is oily in nature, a conclusion which agrees with that of Chodat and other investigators.

If, after removing the red colour as already described, methylene blue is added, the individual cells become dark blue and the general membrane assumes a faint blue tint, showing that pectic substances are present. Under these circumstances the gelatinous material surrounding the cells is seen to be clearly lamellated (Fig. 3 C).

The cells appear to be arranged in groups forming somewhat spherical masses within the enclosing membrane. This feature is also shown by staining with safranin or iodine after removing the greater part of the red oily material. The jelly appears thick and finely

lamellated both round the individual cells and the groups. Colonies of two and four cells having a regular arrangement may be clearly seen, indicating that cell division occurs (Fig. 3 B, D, E). At times the spherical masses of jelly round individuals or groups of cells can be clearly discerned, giving the appearance of frog spawn (Fig. 3 C). It seems probable that the gelatinous membrane is secreted from the individual cells and becomes impregnated with the red oily material, which is probably generated within the cells.

Cultures

All attempts to cultivate *Botryococcus braunii* on agar were without success. In a liquid medium such as dilute Moore's solution (0·1 per cent.) the alga lived for a time, but no observations on the method of reproduction apart from the vegetative division alluded to above have been made. Hence the systematic position of the alga remains uncertain and its assignment to the group of Heterokontae must still be regarded as provisional until definite Heterokontean characters have been established. In this connection attention might be drawn to the presence of oil and the absence of starch in the cells; also to the resistant (probably siliceous) nature of both cell walls and surrounding membranes, a character which is frequent in, though not confined to, this group.

BOTRYOCOCCUS PROTUBERANS W. AND G. S. WEST

Plankton material was examined from Barberspan, S.W. Transvaal. This species agreed with *B. braunii* in chemical characters. The preservation of the form of the masses as well as of individual cells after treatment with strong hydrochloric and strong sulphuric acids was again observed.

A noteworthy feature appeared to be the extreme elasticity of the membrane, the masses expanding considerably on pressing the coverslip. Under these conditions groups of cells with their "stalks" were readily seen. Many of the cells are rather wedge-shaped, others agreed with *B. braunii* in general form (Fig. 3 F). On releasing the pressure both cells and masses quickly resume their original position.

The cells contain bright granules which disappear on warming with strong potash solution. The granules are therefore in all probability oily in nature. As in *B. braunii*, the gelatinous material could be seen round individual cells and also round pairs and groups of three and four cells (Fig. 3 F). Methylene blue stained the cell walls distinctly blue. The general membrane was stained but slightly.

After such staining many colonies consisting of four cells were distinctly visible against the pale background of the membrane.

TRIBONEMA DERBÈS AND SOLIER

The only species of this genus that was found was *Tribonema bombycinum*, which was obtained from Saltenstall Lake, near New Haven, Conn., and from the islands of Cuttyhunk, Pasque, Ferber and Nonamessett, Cape Cod, Mass.

BUMILLERIA SICULA BORZI

Bumilleria sicula was found in moderate quantity in West Park, near New Haven, Conn. This is probably the first record of its occurrence in the U.S.A., though it is probably more common than is supposed as it is likely to be overlooked when growing with other filamentous algae. The filaments, which are free-floating, usually have H-shaped ends, and show a marked tendency to dissociate into fragments, which also have H-ends (Fig. 4 H, J). They are generally irregular and are often much contorted: this appears to be due to the unequal thickening of the cell membrane. The dimensions of the cells are: length, $14–18\mu$; breadth, $10–12\mu$. Of frequent occurrence are chains of short, almost rectangular cells which lie between separated H-pieces (Fig. 4 L, M, P). These appear at intervals in the filaments, and are formed by a series of cross-divisions. No vertical walls resulting in two rows of cells, as described by Borzi, were seen.

The cell walls are highly pectic, as is shown by treatment with methylene blue. Occasionally the membrane is seen to be distinctly lamellose even in the natural state (Fig. 4 J). However, on warming with caustic potash no further change is apparent.

The cells usually contain numerous minute granules which are often very clear and shining. In addition there are one or more fairly large globules (Fig. 4 H). When warmed with caustic potash all the granules run together, while the application of carbon disulphide causes the complete disappearance of all granules, large and small. Sometimes there are present in addition a number of rather prominent whitish bodies as in *Tribonema*. These probably consist of leucosin. In each cell are several parietal chloroplasts (Fig. 4 H), but at times the individual chloroplasts are not discernible, the cells appearing uniformly yellow-green. Strong hydrochloric acid causes the contents to become blue-green, showing the presence of xanthophyll. On warming alternately with strong hydrochloric and strong

sulphuric acids the whole filament disappears, proving that the cell walls are devoid of silica.
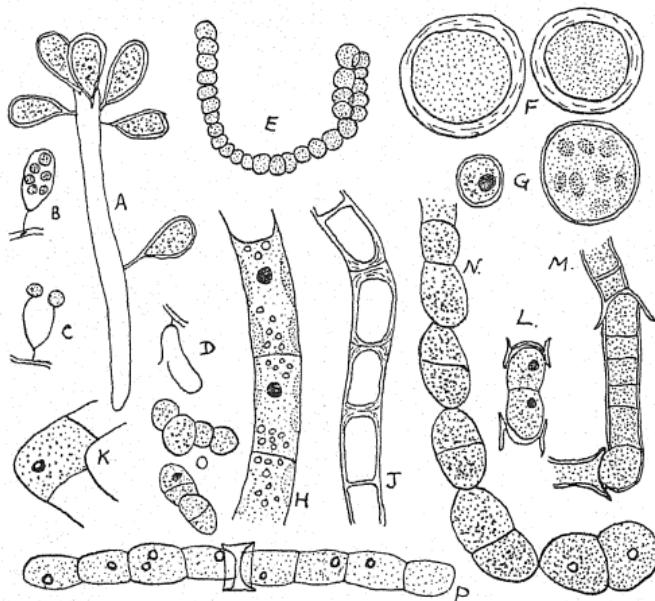
Fig. 4. A–E, *Ophiocytium arbuscula*. F, G, *Botrydium granulatum*.
H–P, *Bumilleria sicula*.

A. *Ophiocytium arbuscula*. Young plants growing on empty cell. ×500.
B. Cell containing zoospores. ×500.
C. Empty cell after the discharge of zoospores. ×500.
D. The same.
E. Cell converted into a chain of akinetes. ×500.
F. Cysts of *Botrydium granulatum* with thick wall—one with brick-red contents. ×500.
G. Akinetes (or aplanospores). ×500.
H. *Bumilleria sicula*. Vegetative filament. ×900.
J. Filament showing layering of the membrane. ×750.
K. "Knee bend." ×750.
L, M, P. Series of cells in filament within H-pieces. ×500.
N. Filament breaking up into akinetes. ×750.
O. Fragmenting filaments. ×500.

Occasionally one or two small but distinct red spots are observed within the cell, but this is by no means a constant feature. Iodine solution causes the granules to become dark brown, but no trace of starch is observed.

Reproduction

"Knee bends" are common as in *Tribonema*, especially in cultures, the cell at the angle of the knee often enlarging to form an akinete (Fig. 4 K). Vegetative division of the cells of the filament is very common, one cell dividing into a series of cells, usually six to eight or more, which form a complete series within the now separated H-pieces, these latter being part of the original cell (Fig. 4 L, M, P). A filament often consists of a series of such segments, separated by H-pieces. These are occasionally zig-zag, the angles coinciding with the separated H-pieces.

The filaments frequently break into a series of barrel-shaped sections, each consisting of a chain of oval cells, each of which divides into two cells, which become akinetes (Fig. 4 N). Aplanospores are formed as in *Tribonema* by the cell contents becoming rounded off. These are liberated by the breaking of the filament into H-shaped pieces, which often appear to be layered.

Cysts are formed, probably by the development of a thick membrane round an ordinary cell which has become detached from the filament as an akinete. These are large and globular, with yellow-green contents and a prominent spot near the centre. The contents are very granular and in some cases they are distinctly reddish in colour. The cyst is invested with a thick transparent wall which is sometimes lamellose.

No zoospores were observed, though they have been recorded by several investigators. Borzi[1] figures one cilium only, but Pascher[2] states that there are two unequal cilia. The zoospores are said to be very amoeboid.

Cultures

Bumilleria sicula was readily isolated from its associates and grown without difficulty on agar, on which it forms an irregular yellow-green incrustation. The alga also appeared to thrive in liquid cultures, e.g. Detmer's solution ($\frac{1}{4}$ or $\frac{1}{10}$). All types of reproduction with the exception of zoospores were very frequent in the cultures, akinetes—both in chains and at "knee bends"—aplanospores, and cysts, being commonly observed.

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[1] *Studi Algologici*, Fasc. II, Tav. XVI.
[2] *Süsserwasserflora*, Heft II, S. 108.

BUMILLERIA EXILIS KLEBS

This species was found in small quantity in several localities near New Haven, Conn. The alga is in the form of a very slender filament which has a thickness of about 6μ. The cell walls are very thin and delicate and stain very readily with methylene blue, showing the presence of pectic compounds. The wall shows no layering when treated with caustic potash. The filaments often end in **H**-shaped pieces, but there is little or no tendency to irregularity or contortion of the filaments as in *B. sicula*. A relatively large proportion of xanthophyll is present, as is shown by the instant appearance of the blue-green colour when treated with strong hydrochloric acid even in the cold. The filaments appear to fragment very readily into smaller segments.

Reproduction

Filaments were observed dissociating into **H**-shaped pieces, the contents of the individual cells becoming rounded off. These were doubtless aplanospores. No zoospores were seen.

BOTRYDIUM GRANULATUM (WALLR.) GREV.

This very cosmopolitan alga was found abundantly both in the environs of New Haven, Conn., and of Wood's Hole, Mass. My observations of the alga did little more than confirm those which have already been made by other investigators. The following points however may be added.

In a liquid culture of *B. granulatum* (Detmer, $\frac{1}{5}$) chains of akinetes were found, which were formed by the division of the rhizoids after the migration of the contents of the coenocyte had occurred. Each akinete was provided with a strong wall and was sometimes slightly barrel-shaped. The contents were granular with numerous distinctly yellow-green chloroplasts (Fig. 4 G). A large colourless spot was often present in the cell. A very striking family likeness was observable between these cells and typical unicellular Heterokontae.

Cysts

Cysts with a thick colourless pectic wall were formed in a culture of *B. granulatum* on peptonised agar (Fig. 4 F). These at first have bright green contents which afterwards become changed to a brick-red colour. The size of the cysts varied from 24μ to 38μ in diameter.

Zoospores

Zoospores of *B. granulatum* have been described from time to time by various investigators. In these one cilium only is usually recorded. Kolkwitz[1] however has described and figured zoospores with two unequal cilia, the longer one being stated to be eight times the length of the shorter one. These observations were made on fresh material which was admittedly mixed with other algae. As Kolkwitz states that some of these zoospores were actually seen while still within the coenocytic membrane it seems possible that they belonged to *B. granulatum*. I have been unable to observe zoospores under conditions of pure culture so far. However, in fresh material cultivated in sterile Detmer's solution ($\frac{1}{3}$) I have observed zoospores in which cilia of unequal length were seen.

If this question of the zoospores may be regarded as settled, then the often-questioned position of *B. granulatum* as a member of the Heterokontae is entirely established. The disc-like chloroplasts, the presence of a large amount of xanthophyll and the unequal cilia determine its position unequivocally.

EXPERIMENTS ON THE CHLOROPHYLL OF TYPICAL HETEROKONTAE

I. *Extraction of xanthophyll and carotin from* Chlorobotrys stellata

A large quantity of this species was found growing very freely and in a relatively pure state on the sides of a plant pot in the Yale University greenhouse. This was collected and carefully washed through pure acetone on a Büchner funnel. The process was continued until the filtrate was colourless. The acetone extract was then transferred to a separating funnel containing ether. A 30 per cent. solution of alcoholic potash was added and the whole was vigorously shaken. The green pigments are saponified by the alkali and form a green solution, which falls to the lower part of the funnel, and so can be withdrawn. The process was repeated several times until the upper liquid became a clear amber colour. This contains the xanthophyll and the carotin in solution. To demonstrate this, to a small quantity of the yellow solution a few drops of strong sulphuric acid were added. The characteristic blue-green colour appeared after a few moments: similarly with strong hydrochloric acid, when a very distinct blue-green colour was evident after warming for a few moments.

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[1] "Zur Ökologie und Systematik von *Botrydium granulatum*," *Ber. Deutsch. Bot. Ges.* **44** (8), 1928.

II. *Crystallisation of xanthophyll and carotin within the cells of certain Heterokontae*

(1) A number of healthy filaments of *Tribonema bombycinum* were placed in an alcoholic solution of potash (20 gm. of potash to 80 c.c. of alcohol) and kept in a closed vessel in darkness until the chlorophyll was extracted. Under these conditions carotin and xanthophyll remain within the cells. The filaments were then washed with distilled water for about twelve hours, and afterwards were mounted in glycerine on a slide. At the end of one to two days, crystals of xanthophyll and carotin appeared very clearly in the cells. The former had the appearance of yellow plates of irregular shape, while the latter were in the form of smaller red plates. Almost every cell of the filaments contained one or more crystals. Should the cells contain much oil, the carotin may not appear—or very little only—since the crystals are soluble in oil.

(2) A precisely similar experiment was made, using filaments of a typical green alga (*Spirogyra*) instead of the Heterokontean species. The result was in striking contrast, as only occasionally was a cell seen to contain one or several yellow or red plate-like crystals. The majority of the cells showed none whatever, thus demonstrating in a striking manner the larger proportion of the yellow and red pigments in the chlorophyll of *Tribonema*.

(3) A similar procedure was followed, using cells of *Chlorobotrys stellata* from the source mentioned above. The pectic material causes the cells to adhere in masses, so that with care these can be transferred from one liquid to another. At the end of the process, minute but distinctly reddish plate-like crystals could be seen in a number of the stellate cells. This experiment was repeated, using a sample of *C. stellata* obtained from a different locality. A precisely similar result was observed.

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STUDIES IN TRANSLOCATION

II. THE MOVEMENT OF FOOD MATERIALS IN PLANTS[1]

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(With Plate I and 7 figures in the text)

I N a previous paper communicated to the Royal Society of Edinburgh[1] I described some experiments which had been carried out with the Swede turnip, with a view to establishing the reasons for the asymmetric development of the bulb. The results obtained in these experiments showed quite clearly that there was a distinct tendency towards localisation in the translocation of the elaborated food materials. It was found that the removal of the leaves from one side of the crown in the early stages of growth resulted in the development of a bulb which was flattened on the defoliated side. It was also shown that a differential exposure to sunlight of the leaves on different sides was associated with the asymmetric development of the bulb. A study of the passage of eosin in the plant was also made, and it was found that the results obtained when this substance was allowed to move in the vascular system confirmed the hypothesis of regional localisation.

The results obtained in this investigation were so striking and so suggestive of a new method of approach to various problems that it was felt desirable to continue the work in other directions: the more so, since this is one aspect of the study of translocation which has, in the main, been neglected in the past. Czapek, in 1897[2], showed that the cutting across of one-half of a petiole of a vine leaf prevented, or, at least, delayed the removal of starch from the corresponding half-lamina. He also showed that where vertical bridges of tissue connected the upper and lower portions of the bark, the effects of ringing were nullified. Oblique and zigzag bridges were ineffective. Dixon[3] has also shown that movement of various substances across a stem is rare and apparently difficult. The work of

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these authors, however, was directed along other lines, and their investigations were not primarily concerned with the study of the section of the organ in which movement took place but rather of the tissues concerned.

It has been customary from the point of view of translocation to regard the plant loosely as a continuous whole, and hence to consider that anything absorbed by the root would pass up the stem more or less at haphazard and, conversely, that the materials synthesised in the leaves would pass generally throughout the plant. A remark in a recent paper on translocation illustrates the kind of outlook not uncommon among botanists. The writers, Mason and Maskell(4), refrain from attempting to work out a formula for the rate of flow through a narrow channel left in a ringed stem because they "could not find any mathematical treatment for the case of a hollow cylinder constricted at a point." The main objection to such a treatment is probably not mathematical but rather physiological, as will be shown hereafter.

The results detailed below show that lateral translocation in the normal plant is even less marked than might reasonably have been anticipated.

An objection which might be raised with regard to the work of the present writer on the Swede turnip cited above is that the results obtained with this material should not be generally applied. The bulb of the Swede turnip is an enormously hypertrophied stem-hypocotyl-root system. The main development is in the region of the xylem tissue, which is very bulky, being largely made up of parenchyma in which are stored the reserve materials, principally hexose sugars. In this ground-mass of parenchyma there are embedded small groups of xylem elements proper, separated from each other by considerable distances in the central portion but more closely grouped together in the region immediately internal to the cambium. There is a single cambial layer from which are derived all the components of the storage tissue. As can be seen, this plant is by no means typical in its structure, and it was felt that other plants should be used in experimentation.

EXPERIMENTS WITH *HELIANTHUS*

The first set of plants to be used was *Helianthus annuus*. These plants were sown in pots in the greenhouse in November. As the young plants grew, leaves were removed, one from each successive pair, so that one-half of the stem was defoliated. It was easy to decide which

leaves to remove in the early stages when the plant has a decussate phyllotaxis, but it became more difficult to make the decision when the leaf arrangement became more complex. This point has been elaborated and a detailed study has been made by Church(5). In this later stage the leaves were removed so as to keep the defoliation roughly to one-half of the stem. The conditions under which the plants grew happened to be unfavourable and the plants remained small and badly developed. When the floral parts were formed it was found that in the uninjured control plants the stem immediately below the capitulum tended to bend over more or less regularly in the direction of incidence of the light. In the treated plants, however, the stem was always bent towards the side from which the leaves had been removed, regardless of the direction of the light. When the flowers of the controls opened, their parts developed more or less simultaneously all round. The ray florets on the lower side of the capitulum of the treated plants, on the contrary, were nearly a week later in development than those on the upper side, and when they did unfold were irregular in shape and position, and very much smaller in size. The plants were all very small and the general growth was much affected by the unsuitable conditions. Measurements of the capitulum were made, the organic centre being taken as the central point. The "radii" A, B, C and D were measured from the centre to the periphery of the disc, the ray florets being ignored. A is the radius away from the defoliated side, B is the radius towards it, while C and D are the two intermediate in position. Details of three typical cases are given in Table I.

TABLE I.

The length of the radii A, B, C and D of the capitulum.

Plant	A (mm.)	B (mm.)	C (mm.)	D (mm.)
Control	11	11	11	11
Treated (1)	18	9	14	14
Treated (2)	13	6	9	9

It will be seen, from the above table, that the axis towards the middle of the side from which the leaves were removed has grown only about one-half as much as the opposite side. It is probable that the difference between the two sides would have been even greater still had not the growth of the whole plant been somewhat curtailed by the reduction of the photosynthetic activity of the remaining

leaves. The plants in this case were about one-fifth of the normal size. The fact that the intermediate radii C and D were equal in size is of interest in the light of the data obtained with *Coleus*, discussed later in the paper.

Other seeds of the same batch were sown out-of-doors in May and the plants were allowed to grow till the end of July. At that time the flower buds were just forming. The leaves were cut off on one side of some of the individuals, which were allowed to continue growth. In these cases, again, there was a distinct asymmetry of the capitulum, the part towards the defoliated side being much reduced. This is of particular interest since the period between defoliation and flowering was comparatively short, being from 4 to 6 weeks. The asymmetry was most marked in the bent region of the stem just below the inflorescence, where the upper side was better developed than was the lower. The first photograph in Pl. I shows the appearance of the capitulum in section.

In the case of some of the plants the lamina of a leaf was removed and the cut end of the petiole was inserted into a tube containing a dilute aqueous solution of eosin. The eosin was drawn backwards into the stem, travelling both upwards and downwards (cf. Caldwell(6)). Within 24 hours the solution appeared in the leaves which were as nearly as possible directly above and below the treated one and in the half-laminae of those on either side. The pattern was not so geometrically exact in this case as in that of plants (e.g. *Hydrangea*) with decussate phyllotaxis, but it was very similar. (It has already been noted that the Sunflower in the early stages has decussate phyllotaxis.) After the lapse of a few days, the eosin finally spread over to and killed the previously unstained half-laminae. At the end of a fortnight when the capitulum opened practically one-half was distinctly abnormal, especially in the sector over the insertion of the treated petiole. Further, the majority of the leaves were shrivelled and dry, except those on the side of the stem opposite to the treated petiole which were, to all appearance, normal.

From these experiments it would appear that the materials which leave any one leaf tend to be distributed in a region of the plant equal in extent to about one-half or one-third of the whole cross-section of the stem. Therefore, one might conclude that any one leaf is directly connected only with one particular sector of the whole stem. In the species employed, in which the phyllotaxis is not decussate in the adult, this region is rather less than one-half of the whole

stem. Nevertheless, the movement of the eosin solution does indicate that the leaves directly above and below the treated petiole are much more intimately connected with it than are those which, though nearer to its place of insertion, stand on different orthostichies. The leaves on the two sides adjacent are connected to the petiole in question by one-half of their vascular system, so that it might be expected that the nearer half of the lamina would become affected with the eosin before the other—as has already been shown to be the case.
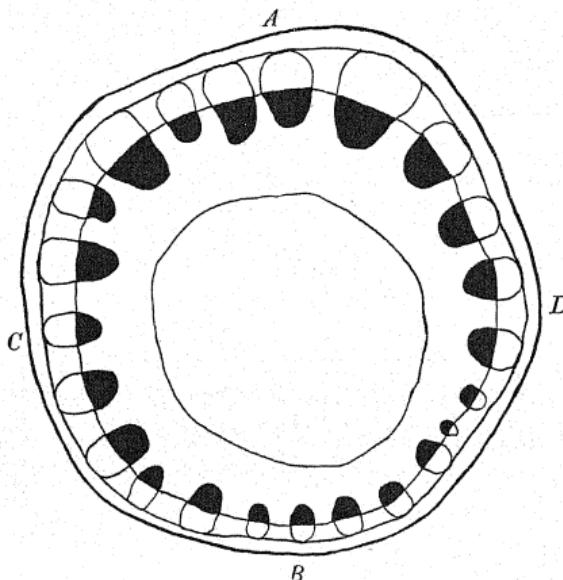
Fig. 1. Diagram of *Helianthus* stem (from camera lucida drawing) showing asymmetric development following defoliation on side *B*.

Further, the writer has noticed in many different types of plants, notably in those with decussate phyllotaxis, that the unconnected half of the lamina in question is stained as a result of the movement of the dye solution into it along the fine bundles which anastomose at the top and edges of the lamina. The eosin evidently has to travel round the lamina before it can reach the petiolar bundles of the opposite side. This phenomenon has also been observed by Dixon in pinnatifid leaves[7] and by the present writer in the case of the diffusion of toxins from parasites of different kinds.

Additional evidence of the differential movement of materials is furnished by the study of the cross-section of the stems of plants which had been grown in the greenhouse in winter. The appearance of such a section is shown in Fig. 1. The bundles on the side A are much better developed than those on the opposite side B, while those on sides C and D are intermediate in size. There is, in fact, a regular gradation in size from the very small bundles at B to the large bundles at A. This is what would have been expected, since B is the defoliated side. The bundles which are intermediate in position have received a small amount of food-material from the leaves which remained on the plant.

EXPERIMENTS WITH PLANTS HAVING DECUSSATE PHYLLOTAXIS

The interpretation of the results obtained with Swede turnips and Sunflowers is difficult by reason of the fact that the leaf-arrangement of these plants is complex. Recourse was, therefore, had to plants with a constant decussate phyllotaxis. The new experiments were carried out with various plants—notably Privet, *Lamium*, *Mercurialis* and *Coleus*.

EXPERIMENTS WITH PRIVET CUTTINGS

Three-year-old cuttings of Privet (*Ligustrum ovalifolium*) which were well rooted were selected. The lower end of the stems was slit longitudinally for a distance of some 2 inches so that approximately the same number of roots were left on either side of the slit. The cuttings were then placed over a plate of glass fixed upright in a box so that one set of roots was embedded in the soil, a rich loam, on one side, while the other set was embedded in sand on the other. Others of the cuttings similarly treated were planted in sand, and still others in soil for use as controls. After a year's growth had taken place it was found that the experimental plants had grown so that the half of the plant rooted in the soil was normal, while the other half was ill-developed, the leaves being small and chlorotic: so much so that the half-plants were indistinguishable from the plants grown on the corresponding soil. This result is in accordance with the results obtained by Auchter (as quoted by Curtis(8)). This clear-cut phenomenon was undoubtedly due to the fact that the phyllotaxis is decussate, since in plants having a more complex leaf-arrangement, e.g. Willows, the end results are not nearly so definite.

EXPERIMENTS WITH *LAMIUM* PLANTS

The lamina of one of the leaves of a *Lamium album* plant was removed and the cut end of the petiole stump inserted into a tube containing a very dilute solution of eosin (0·02 per cent.). After 3 weeks the plant was examined and it was found that growth had resulted in definite asymmetric development. The leaves above the treated petiole had not grown nearly to the same extent as had those on the opposite side. The flower-buds in the axils on this side had not developed at all. On the alternate sides, further, one-half of the cymose inflorescence, that on the side away from the petiole, had developed quite normally and the flowers had opened, while those on the nearer half of the stem remained undeveloped. The stem of the plant was bent towards the side supplied with the eosin. The leaves (see Fig. 2) have been removed from one of the stems, pressed, and mounted on an herbarium sheet. The leaves directly above the treated petiole are very much smaller than those on the opposite side, which are indistinguishable from those of normal plants. The half-laminae on the alternate sides are also much less well grown, especially those towards the top of the plant where the leaves are almost sickle-shaped as a result of the overgrowth of the side which has not received the eosin. The stem of these plants was also much distorted—the appearance in section being shown in Fig. 3 (a). The side nearer the treated petiole had obviously grown much less than had the opposite side, its length in cross-section being about one-half of that of the normal side.

This plant shows very well the absence of easy lateral translocation of materials in the case of plants having decussate phyllotaxis. Similar experiments were carried out with numerous other plants, notably *Mercurialis annuus*, and similar results were obtained. In these cases the bundles were examined in section, and it was found that the eosin had passed only in the bundles of one-half of the stem. The appearance of a section of a *Mercurialis* stem is shown in Fig. 3 (b). In these plants the region in direct connection with any one leaf is equivalent to half the stem.

The above results suggested experiments along new lines, and for convenience *Coleus* plants were chosen. These are suitable both as having decussate phyllotaxis and as being readily grown all the year round under greenhouse conditions.

Fig. 2. Leaves of *Lamium* plant arranged in ascending order. The eosin was absorbed at the petiole of the leaf opposite the lowermost (i.e. older) leaf and moved up on that side.

<p style="text-align:center">EXPERIMENTS WITH *COLEUS* SPP.</p>

The *Coleus* plants were kept in the greenhouse and were available at all seasons of the year. The first experiment was set up on February 18th. For convenience in discussion only the data obtained for one individual will be considered, since these are typical of the data obtained in all cases. The selected plant was a cutting of the previous year and had two small branches each with two smaller
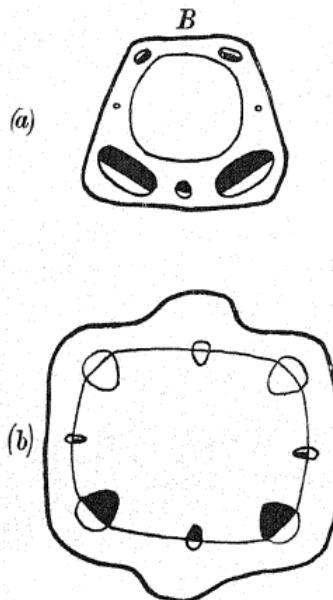
Fig. 3. (*a*) Diagram of *Lamium* stem (from camera lucida drawing) showing non-development of the side *B* on which the eosin had travelled. (The leaves of this stem are those in Fig. 2.)
(*b*) Diagram of stem of *Mercurialis annuus* showing portion of xylem stained in eosin which had been absorbed at the cut end of a petiole of leaf.

branches of the next order growing from it. All the leaves on one of the sets of branches were removed—one odd one and six pairs. The whole branch was then inserted into a small dark chamber made of black paper so that no light could reach the stems. At the time of the setting up of the experiment it was conjectured that most of the reserve materials would already have been used up in the formation of the stems and leaves which had just developed. The branches under treatment made very little growth. A few almost colourless

leaves unfolded slightly and the main stem increased 0·5 cm. in length. After 2 months the cover was removed in order to find out if the stems were still alive. Growth took place almost immediately and at the end of 3 weeks the three pairs of leaves which had developed in the interval were removed from each of the secondary branches and these branches were again covered. As time went on but little
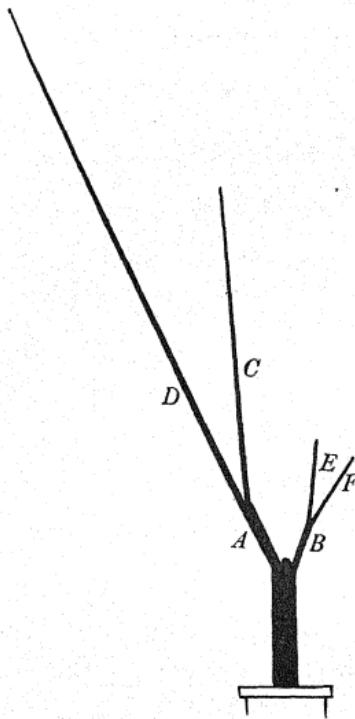
Fig. 4. Diagram of *Coleus* plant (see Pl. I, phot. 2).

growth took place, and at the beginning of August the ends of the secondary branches under treatment were found to be quite dead and shrivelled.

During this time the other fork of the plant had been growing strongly and the appearance of the plant can be seen in the photograph (Pl. I, phot. 2). For simplicity the plant has been represented diagrammatically in Fig. 4. *A* and *B* were the two original branches with the smaller branches *D* and *C*, *E* and *F* on each respectively.
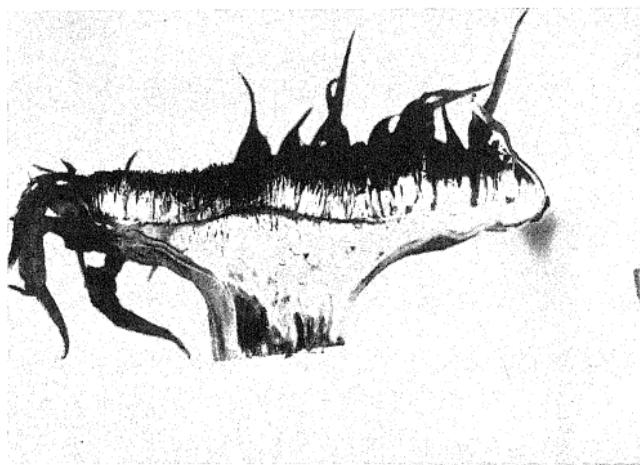
Phot. 1. Photograph of asymmetrically developed *Helianthus* flower showing the organic centre nearer the defoliated left side.

Phot. 2. *Coleus* plant showing absence of growth of the portion which was kept in the dark.
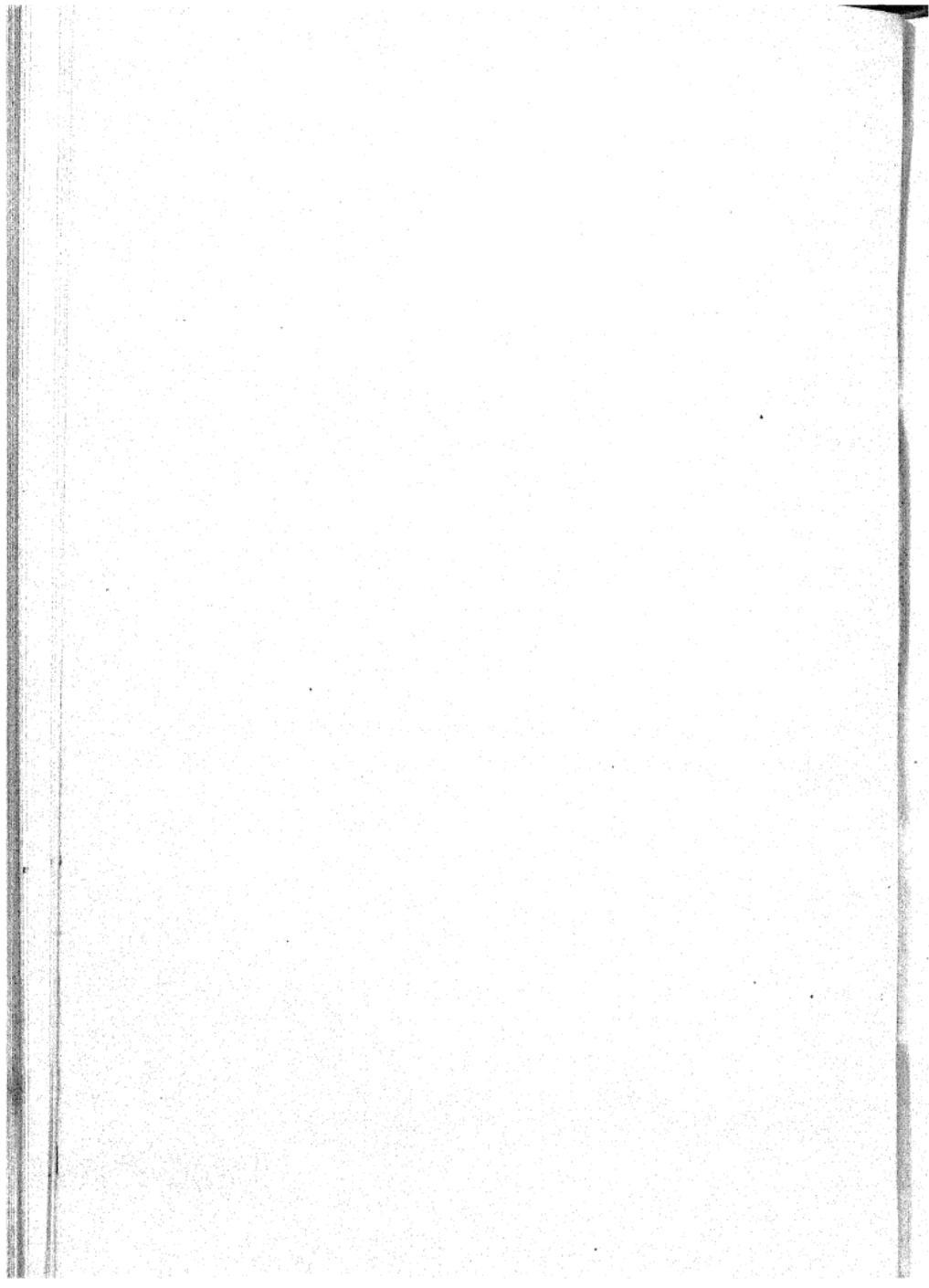
The branches B, E and F were treated as above described. Some of the leaves of the branch C were removed as they developed. One of each pair was removed as they unfolded, always from the same two sides, so that the branch had only one-half of the total number of the leaves on D. The effect of this treatment was seen when flowering took place, as D flowered many weeks earlier than C and was generally a more robust stem. Various measurements were made of the several branches. The data are set out in Table II.

TABLE II.

Measurements made on the branches of *Coleus* after treatment.

Stem	Length in cm.
A	3·5
B	2·5
C	35·0
D	80·0
E	3·5
F	3·5

The weights of the branches C and D were 34 and 70 grm. respectively. Tests were made and starch was found to be present in quantity in the branches A, D and C, but quite absent in B, E and F. Fig. 5 shows the appearance in cross-section of the branches A and B which were equally developed in April, having risen from the same node.

The data given above show that the movement of materials across the plant was so slight as to be negligible, and that each branch in the system was virtually an independent unit as regards the passage of materials. Especially was this so in the case of the covered branches, which were unable to remain alive despite the fact of the presence of large deposits of starch in the branches of the opposite, illuminated side.

The *Coleus* stem is practically square in cross-section and the main vascular bundles are situated in the four angles. The leaves are arranged in four vertical rows and the petiole of each leaf is inserted in the middle of each side of the stem. The two lateral petiolar bundles diverge on entering the stem, and, on going to each of the two nearer corners, there form the half-bundles, each of which is consequently in direct connection with one-half of the lamina. Diffusion across into the other half-bundle is not difficult, however, and the bundles in the corners may be considered as being unit structures. Food materials therefore pass across the bundle quite freely.

If a *Coleus* plant is treated with eosin, as described above, and sections are made of the stem below the treated petiole, some interesting points are to be noted. If the section be cut after 2 or 3 hours the two half-bundles nearest the treated petiole are alone stained. If the sections be cut after 24 hours the whole of the two nearer bundles are stained. Even if the plant be left for some days, however, there is no diffusion across the stem to the other side, nor does
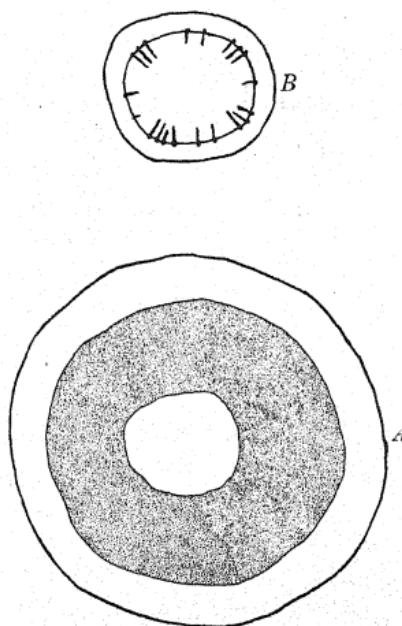
Fig. 5. Diagram (from camera lucida drawing) of transverse section of stems *A* and *B* of *Coleus* plant.

there appear to be any vascular connection which allows of the passage of stains across. When the roots are functioning freely there is probably no diffusion across at all, and the amount of stain which had got across a severed branch under this treatment was, after 48 hours, in a dry atmosphere, so slight as to be negligible. On more than one occasion the whole of one side of a *Coleus* plant has been killed by treatment with eosin while the other side has remained quite normal and continued to grow (cf. the *Lamium* experiments above).

From these observations it would appear that one-half of the stem is more or less in direct communication with the vascular bundles of any one row of leaves. The portion of the stem connected with the rows of leaves on two adjacent sides is represented diagrammatically in Fig. 6. It can be seen that approximately one-quarter of the stem should not be affected if rows of leaves are removed from two adjacent sides. A plant with a four-angled stem is very useful for this kind of experiment since the slightest deviation from the normal development is easily discernible.
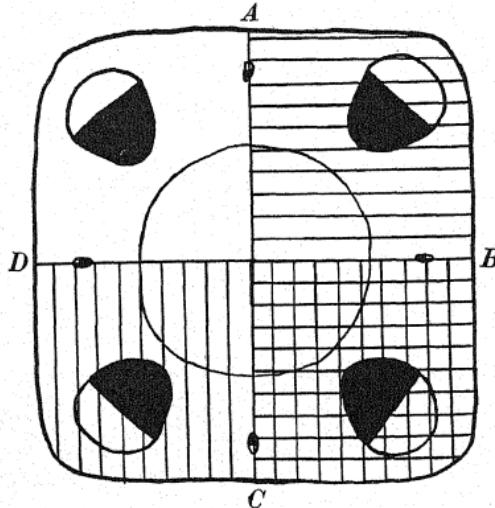
Fig. 6. Diagram of *Coleus* stem showing areas associated with each row of leaves.

Various other experiments were carried out, of which the following may be taken as typical. At the beginning of May a *Coleus* plant with a single stem was selected and the leaves were removed from the two adjacent sides *B* and *C* in Fig. 6. Subsequent growth resulted in an increase in the size of the plant and the leaves which developed on the sides *B* and *C* were removed as they were formed. At the beginning of July the apex of the stem was removed to prevent flowering and to induce the growth of the axillary buds. These grew out of the axils of the leaves on all four sides, but were more conspicuous on the sides *A* and *D*. The lengths of the branches which arose in the several axils were measured and the data so obtained

are tabulated below. It should be noted that one pair of leaves only is developed at each node.

TABLE III.

Lengths in cms. of shoots developed in the axils of leaves.

Node number	A (normal)	B (defoliated)	C (defoliated)	D (normal)
1	45 (f.)	—	Trace	—
2	—	Dead	—	8
3	3	—	Trace	—
4	—	Trace	—	3
5	20	—	Trace	—
6	—	0·5	—	13 (f.)
7	4	—	1	—
8	—	1 (f.)	—	7 (f.)

The nodes were numbered from below upwards: (f.) denotes a flowering shoot. The readings were made on August 1st.

On the same day the shoots 6 *B* and 6 *D* were covered, as described in a previous experiment. It was thought that the material available on the side *D* would obviously be much more in amount than that on side *B*. The plant was put in a warm pit and the subsequent growth was so rapid as to preclude, presumably, much manufacture of food-materials by the leaves themselves.

TABLE IV.

Lengths of the shoots on the sides *B* and *D*.

Shoot number	August 1st (cm.)	August 20th (cm.)
2 *D* (normal)	8	14
4 *D* (normal)	3	11·5
6 *D* (darkened)	13	32
6 *B* (darkened)	0·5	0·7

At this time sections were made just above the second node. The anatomy of the *Coleus* stem will be discussed below. The end of the shoot 2 *D* was also removed just above the first node. The two axillary shoots which arose from this node were allowed to continue growth until October 30th when they were measured. The shoot which had arisen on the side of the branch towards the side *A* of the main stem was 31 cm. long, while that on the opposite side was 3 cm. long. This difference indicates that there was much more food-material available on the side *A* than on the other side *C*.

When the plant was uprooted and examined it was found that there were four rows of roots—one at each of the angles of the stem. The roots which arose from the angle between *B* and *C* were very

small and few in number. Those at the opposite corner were most highly developed and the alternate rows were intermediate in size.

DISCUSSION

The results of the experiments outlined above show that in the case of salts and of elaborated food-materials, at least, the amount of lateral movement is very slight in the plants under investigation. It is suggested that this is also true in the case of all the higher plants, since quite a large range of plants was used as experimental material. There does not seem, however, to be so much difficulty in the lateral movement of water, which appears to move across the plant with almost the same freedom as it moves upward or downward. The experiments of Hales (*Veg. Statisks.* 1769) first demonstrated what is now common knowledge, viz. that water travels apparently down the xylem tract as readily as upwards. Numerous experiments which have been carried out by various workers since have not yielded any evidence which suggests that there is much opposition to the lateral movement of water in the normal plant. Some experiments which I have carried out with bulky storage organs, e.g. Apples and Swede turnips, have given some indications of a differential movement of water in the different directions along the tissues, but the results are not yet sufficiently definite to warrant a statement on this subject. It is felt, however, that the almost complete absence of lateral translocation of other substances has been clearly demonstrated in the above experiments. It appears that this phenomenon is general in all plants, although the interpretation of the results is simpler in the case of those with decussate phyllotaxis.

The stem of *Coleus* presents some interesting features which merit more detailed consideration. As stated above, the stem of this plant is practically square in cross-section. The main vascular tracts are grouped into bundles situated one in each corner of the stem. It has been found that the removal of leaves on two adjacent sides leads to the subsequent asymmetric development of the stem. If one assumes that the leaves on the sides B and C in Fig. 6 were removed, then the vascular bundle in the angle between A and D would not be directly connected with any disturbance in the movement of materials which might result therefrom. If there were absolutely no lateral translocation, therefore, this bundle would be normally developed, that directly opposite would be rudimentary, and those intermediate in position would be intermediate in size, both being of the same dimensions. On examination of the stem of plants so treated this

condition was regularly found. One of the bundles was very large, being equal in size to the bundle in the normal stem, the opposite one was very small and the other bundles were intermediate. Those differences apply to both the numbers of the cells and the sizes of the individual cells making up the bundles.

On an examination of the sections in this connection, it was noticed that the four main bundles and the variable number of smaller bundles are connected in the mature stem by a tissue initiated by the activity of an interfascicular cambium. The feebly
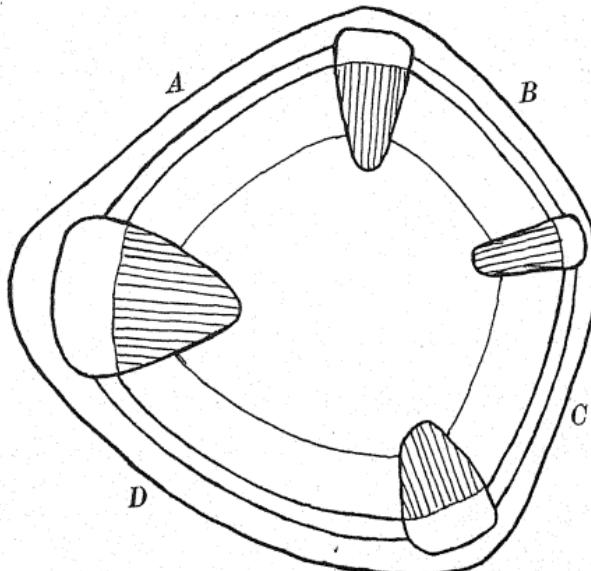
Fig. 7. Diagram (from camera lucida drawing) of transverse section of *Coleus* stem defoliated on two sides.

lignified xylem of this tissue apparently functions as a storage region. This tissue appears to constitute the genuine cauline bundle, and not to be associated with the common bundles which occur in the angles of the stem and as smaller groups on the sides. Support is lent to this contention by the fact that this cauline bundle area is equally developed all round the stem, even in an asymmetrically grown plant as shown in Fig. 7.

A point of more than passing interest in connection with the vascular anatomy of the *Coleus* is that the petiolar bundles consist of two large lateral bundles and a very small median. This unusual

feature is apparently directly connected with the fact that the petiolar bundles in the main join up in pairs to form the common bundles in the angles of the stem.

SUMMARY

The results of experiments on the translocation of materials in the plant are discussed in this paper. These experiments were carried out mainly on plants with decussate phyllotaxis and were intended to extend the work previously carried out on Swede turnips. It is shown that in the Sunflower (*Helianthus annuus*) asymmetry of the stem and capitulum follows on the removal of leaves from one side of the stem. In plants with decussate phyllotaxis the results are even more striking. Using the Privet (*Ligustrum ovalifolium*) it was possible to show that considerable differences in the foliage on each side resulted from the differential treatment of the roots on either side of two-year-old cuttings. The effect of a dilute eosin solution on one side of a *Lamium album* plant was to retard the growth of the leaves and half-laminae on that side and to prevent the development of flowers in their axils. Similar results were obtained with *Coleus* plants which have a stem well suited for this kind of experiment, since the four main vascular bundles are situated one in each corner of the stem. When the leaves of the two adjacent sides were removed as they appeared, it was found that the vascular bundle in that angle remained small and that there was little cambial activity present.

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ILLUSTRATIONS OF CARPEL POLYMORPHISM
V

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(With 13 figures and 19 diagrams in the text)

AMONG the earliest forms to be examined from the new viewpoint of polymorphism of the carpels were various representative genera of the several families included among the Rhoeadales, in particular Papaveraceae and Cruciferae. These investigations led to the conclusion[1] that *parietal* placentation in the original meaning of the term was not a reality in any of these cases except, as it seemed, in one, or possibly two genera of the Papaveraceae, viz. *Platystemon* Benth., in which the ovary has all the outward appearance of being composed only of valve carpels, and perhaps also *Platystigma* Benth. These two genera stand apart from all other members of the Papaveroideae in regard to the position of the stigmas which *alternate* with the placentae. In other words *the stigmas are not commissural*.

According to both Hooker[2] and Baillon[3] non-commissural stigmas also characterise the genus *Romneya*, which is classed in the same section as *Platystemon* and *Platystigma*. But in fact this is not the case. The discrepancy is probably due to the fact that in this genus it is scarcely possible by mere inspection to determine the real relation of stigma to placenta, i.e. whether alternate or superposed, owing to the whole surface of the ovary being densely covered with long, stiff, adpressed hairs which obscure all structural boundaries (Fig. 4). The difficulty is further increased by the fact that the here erect and free stigmatic lobes very generally turn slightly sideways to become fitted among one another. But serial transverse sections show quite clearly that they are the continuations of, and are superposed upon, the placentae (Fig. 12); which is to say, in the phraseology of the polymorphic theory, that they are borne by a whorl of

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[1] Following inevitably from the interpretation adopted. (See "A Reversionary Character in the Stock, etc.," *Ann. Bot.* 37, 451; "Some Conceptions of the Leaf-member, old and new," *Journ. Roy. Hort. Soc.* 50, 241; "Carpel Polymorphism, I," *Ann. Bot.* 39, 123, and later papers.)
[2] *Gen. Pl.* 1, 49. 1862.
[3] *Nat. Hist.* 3, 128. 1874.

fertile, consolidated carpels as in the rest of the Papaveraceae[1]. Hooker's statement appears the more curious as Harvey[2], who originally described the genus, distinctly states that the fleshy, subulate stigmas *are opposite the placentae*.

As the present work progressed, and as it came to be established that the valve type of carpel bears no more than one row of ovules on each margin, the question whether the ovary of *Platystigma* could be interpreted in the traditional way as being composed entirely of valve carpels, and as being a genuine case of parietal placentation, became increasingly doubtful, for early illustrations of one species at least out of the three—*P. lineare* Benth. (*Hesperomecon linearis* Greene)—show the placentae with the ovules in several rows[3]. Unfortunately all efforts at that time to obtain suitable material of *Platystigma* for investigation of the ovary were unsuccessful, and here the question as regards this genus had for the time being to be allowed to rest.

Recently, however, I have had the good fortune to receive from Professor F. E. Clements, to whom I am very much indebted, material of *Platystigma lineare* in flower and in fruit. Examination of this material has now cleared up the situation in regard to this type, and has had the further consequence of removing all doubt in regard to *Platystemon*[4] and bringing the two genera into line.

The ovary of *Platystigma lineare* is surmounted by three (or occasionally four) erect stigma lobes (Fig. 1) *alternating* with as many placentae, and in this latter respect it agrees with *Platystemon*. The ovules are undoubtedly borne in many rows (Fig. 7), as originally shown in the illustration accompanying Lindley's description[5], a fact which at once indicates that fertile carpels of the consolidated type are to be expected. Cross-sections of the ovary base show six residual bundles for the gynoecium on six equidistant radii (Fig. 5). On three of these radii are simple bundles which pass out from the ring, and turning upwards continue to the tip of the stigmatic lobes, constituting the unbranched midribs of as many sterile carpels (Fig. 2). Each of the other three vascular bundle masses supplies an alternate, fertile carpel and branches copiously in fan-like fashion

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[1] The case of *Eschscholtzia*, where stigmas are sometimes borne by the valve (sterile) carpels as well as by the solid members, has been dealt with elsewhere (see *Ann. Bot.* 37, 469, 479; 39, 133, 134; 41, 616, 617; *New Phytol.* 27, 53, 54).

[2] In Hooker's *London Journal of Botany*, 4, 74, 75. 1845.

[3] See Hooker, *Icones*, 1, 38, and *Bot. Reg.* 23, 1954.

[4] Till now in question. See *New Phytol.* 27, 55.

[5] *Bot. Reg. loc. cit.*

in its upward course (Fig. 3). In the fruiting stage the two systems
may become interconnected much in the same manner as has been
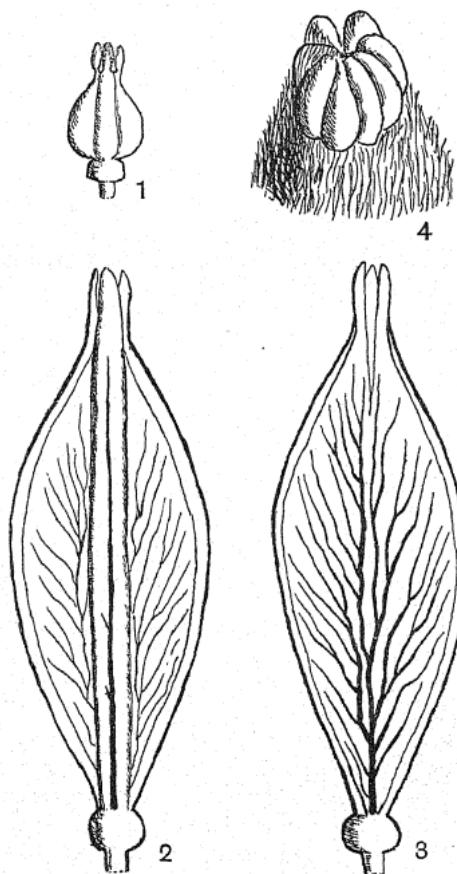
Figs. 1–4. *Platystigma lineare* Benth. 1. Gynoecium from an open flower
    (×6).   2, 3. A fruit, 2 with one of the sterile, 3 with one of the fertile
    carpels in face view (×6). 4. *Romneya Coulteri* Harv. Upper portion of
    young fruit showing the stigma lobes.

shown for cruciferous types (e.g. *Capsella, Iberis*)[1], where the carpel
relations are somewhat similar. Above the ovule region the vascular
tissue of the fertile members is reduced to twin bundles, between

[1] *Amer. Journ. Bot.* **16**, 136, Figs. 11, 12.

which the split occurs when dehiscence takes place (Fig. 8), as is so frequently the case in carpels of the consolidated type. The close-packed stigmatic lobes are centred over the sterile carpel cords, and each receives in addition to this cord one of the twin bundles (half cord) from the fertile member on each side. Each stigmatic lobe is thus the continuation of $\frac{1}{2}$ 1 $\frac{1}{2}$ carpels (Figs. 9, 10). The whole inner surface of the lobe is covered with papillae, and as the edges are somewhat reflexed the papillae can be seen down each side when the lobe is viewed from the back (Fig. 10).

It is thus apparent that the syncarpous ovary of this species is not composed of three fertile valve carpels but of three solid, or very contracted, sterile valve carpels alternating with three fertile, semi-solid carpels (G 3 + 3).

In view of this new evidence it was clearly desirable to re-examine the case of *Platystemon*, since the close relationship of these two genera would lead us to expect the same type of construction in the gynoecium of both. The valve-like appearance of the several component members of the ovary looks convincing enough, but as we have learned, this outward appearance is not infrequently deceptive, as e.g. in Leguminosae, some Rosaceae and Oxalidaceae, and Butomaceae among others. On the other hand, the arrangement of the ovules in several rows on each placenta, as shown in Eichler's[1] familiar and oft-reproduced diagram, seemed at first to constitute a difficulty in the way of an all-valve carpel interpretation. This difficulty, however, at once disappeared on investigation, for, as explained in an earlier account, this simulation of several rows no doubt arises through some of the ovules being enclosed in the bays formed by the (supposed) valve carpels, while others come to be directed at various angles into the common central cavity[2]. Payer's[3] definite statement that the ovules are disposed in only two rows seems to have been overlooked both by Eichler and his successors. So far, then, as outward appearance, ovule arrangement and stigma position are concerned, the evidence is quite consistent with the traditional view; while, as regards the vascular anatomy, the arrangement seen in the ovule-bearing region appears capable of reconcilement either in accord with this view or with a polymorphic interpretation[4]. Pending decisive evidence on this latter point the question evidently could not be settled. This evidence is forthcoming, however, when serial

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[1] *Blüthendiagramme*, 2, 189, Fig. 79.
[2] See *New Phytol.* 27, 54, Fig. 28, and 57.
[3] *Organogénie*, 1, 221.   [4] See *New Phytol.* 27, 55.
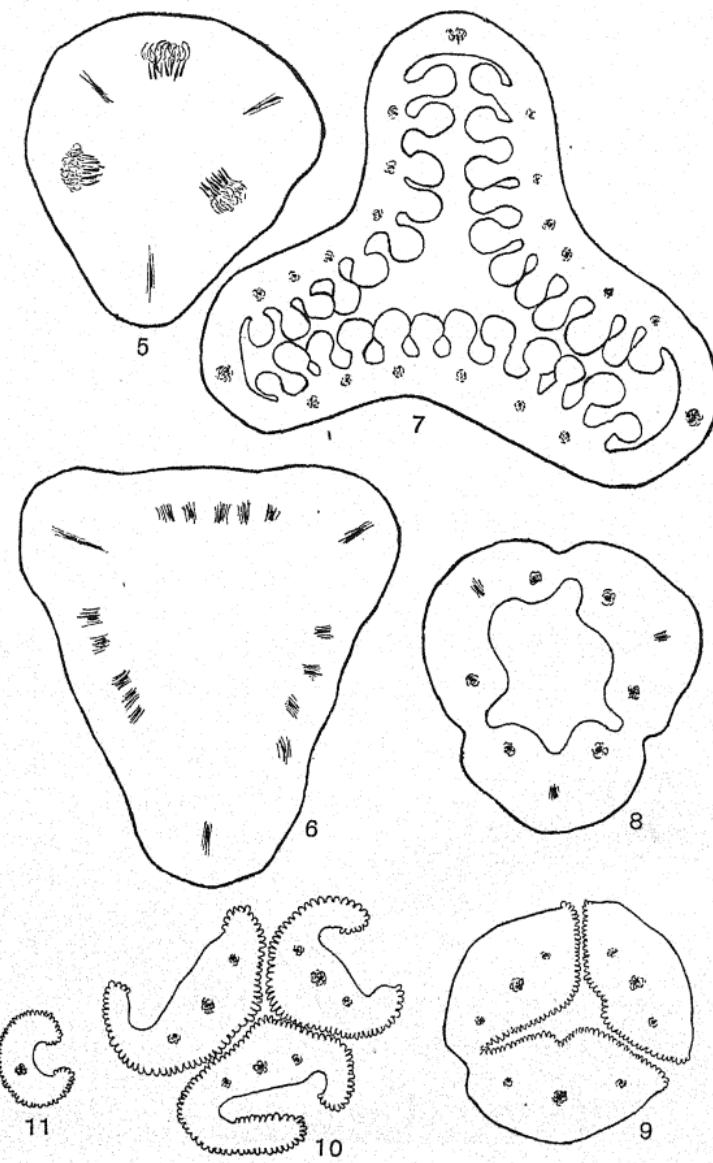
sections are taken through the ovary base. These show that as a rule from six to twelve, but sometimes as many as twenty, sterile and unbranched vascular cords pass out from the central ring, while on the alternate radii are a corresponding number of bundle masses which retain their central position (Fig. 13). Each bundle mass gives rise to the twin fertile bundles seen at a higher level, which represent the mid-vein of a consolidated, fertile carpel. From these twin bundles numerous branches are given off as in *Platystigma*, those from one bundle of the pair extending into the "valve" wall on the right, those from the other similarly into the "valve" wall on the left. From these facts it is clear that the construction here is on the same plan as in *Platystigma*, half the number of carpels being sterile and either of very contracted valve form or possibly solid, the other half being fertile and semi-solid. And so the last remaining case for an all-valve carpel interpretation of the papaveraceous gynoecium falls to the ground, unless it should prove—but this is in the highest degree unlikely—that the vascular anatomy of *Platystigma californicum* Benth. (*Meconella californica* Torr.) or *P. oreganum* Benth. (*M. oregana* Nutt.) differs profoundly from that of *P. lineare* Benth.[1] *Platystemon* also agrees with *Platystigma lineare* in having the stigmas composed of $\frac{1}{2}$ 1 $\frac{1}{2}$ carpels and centred over the sterile carpels, and further, in the median splitting, sooner or later, of the fertile carpels.

Figs. 5–11. *Platystigma lineare* Benth. All from transverse sections taken at successively higher levels. 5. Ovary base below the level of the loculus showing the three outgoing cords for the three sterile carpels and the three large vascular masses for the three fertile members. 6. The same after the fertile carpel cords have begun to break up into the series of bundles which supply the extended placentae. 7. Middle region of the ovary. The sterile carpels occupy the rounded angles, the fertile carpels the whole extent of the sides which bear about a dozen rows of ovules. 8. Ovary above the ovule-bearing region. The vascular system of each fertile carpel is now reduced to twin bundles. The ovary wall is constricted between the two bundles of each pair owing to the formation of a furrow on the outer surface and a bay-like extension of the central cavity on the same radius. The original bays on the alternate radii are, on the other hand, becoming flattened out. These constrictions indicate the points at which dehiscence takes place later. 9, 10. The three stigma lobes becoming distinct through the opening of the loculus on to the exterior. 11. A single stigma lobe after the two half-carpel cords have come to an end leaving only the sterile carpel cord. [N.B. For convenience of arrangement the orientation of Fig. 7 has been reversed as compared with the rest of the series in which a fertile carpel is shown in the mid-line at the back and a sterile one in front.]

[1] Suitable material of these two species has not yet been obtained.
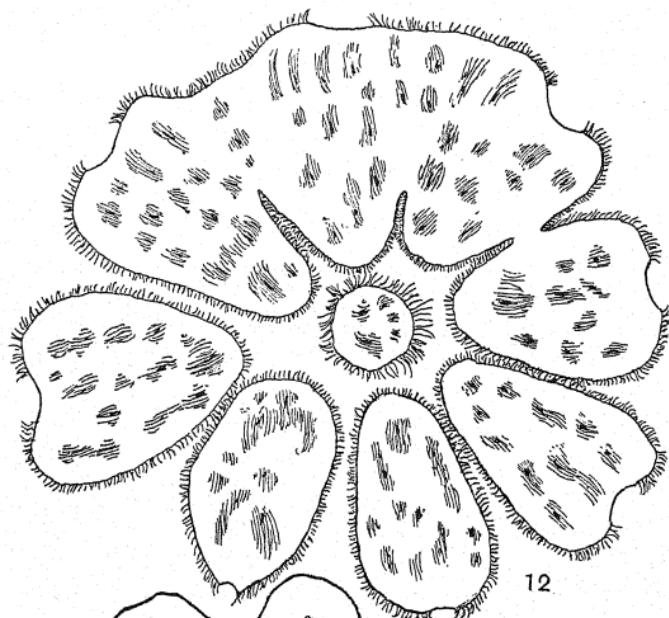
12
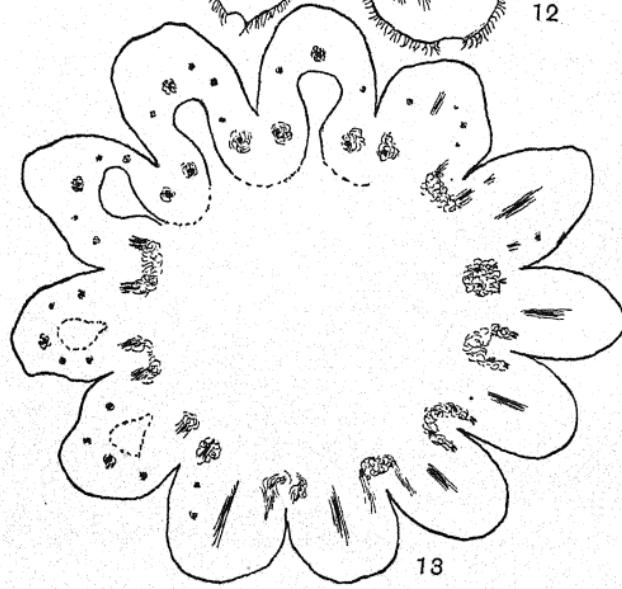
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The conclusions to be drawn from the foregoing account of the constitution of the gynoecium in certain papaveraceous types may then be stated as follows.

CONCLUSIONS

1. All papaveraceous types so far investigated show polymorphism of the carpels; that is to say, in none does the gynoecium consist of valve carpels only. [*Platystigma californicum* Benth. (*Meconella californica* Torr.) and *P. oreganum* Benth. (*M. oregana* Nutt.) have not yet been examined.]

2. It follows from the above that true parietal placentation in the original sense of the term does not occur in any of these types.

3. In *Platystigma lineare* Benth. $G = 3$ sterile, very contracted valves (or possibly 3 solid carpels) + 3 fertile, semi-solid; in *Platystemon californicus* Benth. $G = 6$–12–20 very contracted, sterile valves + 6–12–20 semi-solid and fertile.

4. The stigmas in all Papaveroideae (*Romneya coulteri* Harv. included) are commissural except in *Platystemon* and *Platystigma*, where they are centred over the sterile carpels (in other words, are alternate with the placentae), and in some flowers of *Eschscholtzia* (previously described)[1], where they are developed on the valve as well as on the solid carpels.

5. In the two exceptional species mentioned in para. 3, in which the stigmatic filaments or lobes alternate with the placentae, each stigma receives the whole vascular cord of a sterile carpel and the

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Fig. 12. *Romneya coulteri* Harv. Transverse section of the ovary apex at the level of origin of the stigmatic lobes. The sterile carpels have come to an end with the result that already five of the eight loculi communicate with the exterior. Each of the separate structures (fertile carpels) continues upwards, becoming the superimposed stigma lobe, with one of which the central column of residual tissue later becomes merged. [For the appearance at the ovary base showing the sterile as well as the fertile carpel cords, see vol. **27**, 54, Fig. 29.]

Fig. 13. *Platystemon californicus* Benth. Transverse section through the ovary base; the carpels on the one side are slightly further developed than on the other. On the right the sterile carpel cords are seen passing out horizontally, on the left they have resumed an upward course and are cut transversely. Three loculi have made their appearance and two others are becoming defined. Ground tissue still occupies the whole of the central area so that these chambers do not yet communicate with one another. The vascular system of the fertile carpels, lying on the alternate radii, is seen, in one case as a single cord (right), and in the remainder in various stages of differentiation into twin bundles which supply the ovules, and from which the secondary veins take their rise.

[1] See *Ann. Bot.* **37**, 469 and 479; and **39**, 133 and 134. Also *New Phytol.* **27**, 53 and 54.

half cord or half group of bundles of the neighbouring fertile carpel on each side. Each is thus composed of $\frac{1}{2}$ I $\frac{1}{2}$ carpels.

6. The formation of these separate compound stigmas comes about through the median longitudinal splitting of the fertile carpels in the stigmatic region.

7. Dehiscence of the fruit in *Platystigma lineare* is due to the extension of this split down the ovary wall; in *Platystemon* the extension of the split leads to the separation of each $\frac{1}{2}$ I $\frac{1}{2}$ carpel combination which forms a closed structure. In other papaveraceous types splitting occurs either between the individual valve and solid carpels, whether four (*Chelidonium* type) or more than four (*Papaver* type); or between the two median fertile carpels and the whole block of the sterile valve and solid carpels on each side (*Eschscholtzia* and allied forms).

8. In *Romneya* the ovary is plurilocular owing to the presence of a persistent central core containing vascular elements. These vascular elements are not utilised in the construction of an additional carpel whorl but eventually become merged with those proper to one of the original stigmatic lobes.

DIAGRAMMATIC REPRESENTATION OF FLORAL STRUCTURE IN ACCORD
WITH THE CONCEPTION OF CARPEL POLYMORPHISM

Now that the case of *Platystigma* is satisfactorily cleared up, the present seems a fitting moment to indicate by the method of floral diagrams the modification in our conception of the construction of the syncarpous gynoecium entailed by adoption of the view of carpel polymorphism. The diagrams which follow represent the chief types of gynoecium (indicated by small letters) occurring among the Papaveraceae and Cruciferae. For completeness the outer floral whorls are also shown in each case (indicated by capital letters), but, from considerations of space, separately, and on a smaller scale.

The accompanying drawings were made by Miss D. F. M. Pertz, to whom I wish to express my very grateful thanks.

Floral diagrams of various Papaveraceae and Cruciferae
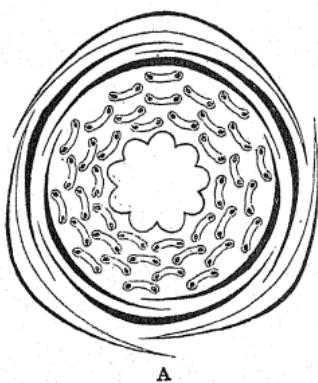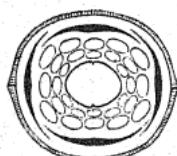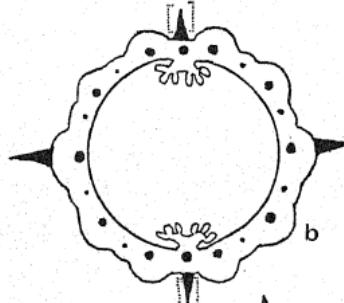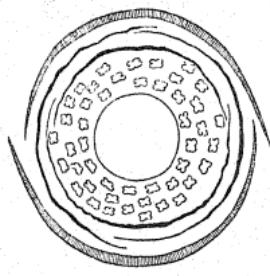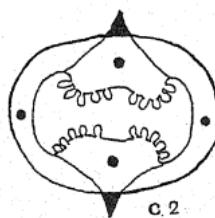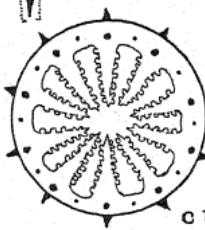
A, a.   *Platystemon.* $G\,9+9$. Stigmas non-commissural. Ovules in two rows.

B, b.   *Eschscholtzia.* $G\,20$ (full ground plan $12+12$). Stigmas, when two, non-commissural, when more than two, both commissural and non-commissural. Ovules in numerous rows.

C.   Common papaveraceous type.

c 1.   *Papaver.* $G\,10+10$. Stigmas commissural. Ovules in numerous rows.

c 2.   *Glaucium flavum.* $G\,2+2$. Stigmas commissural. Ovules in numerous rows.

D   d 1   d 2

E   e 1   e 3

e 2   e 5   e 4

e 6   e 7   e 8
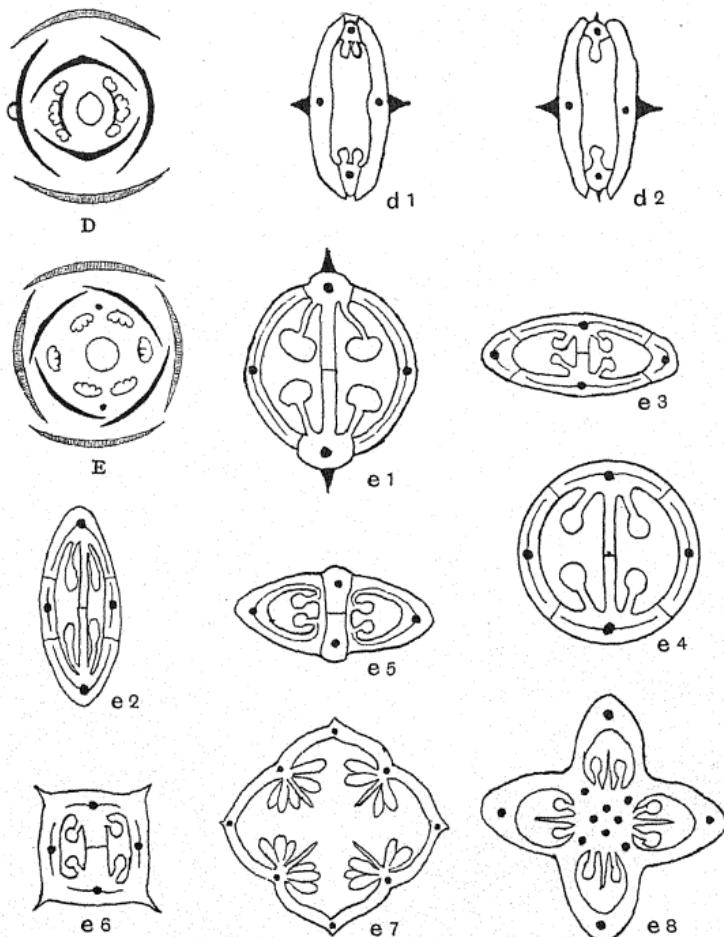
D, d 1, d 2. *Corydalis*. G 4. Stigmas two non-commissural ± two commis-
          sural, non-functional (d 2). Ovules in two rows (d 1) or in a single
          row on each placenta (d 2). d 1, *C. cava*; d 2, *C. lutea*.

E.   Typical crucifer.

e 1.   *Cheiranthus* (siliqua). G 4 (two valve, sterile; two solid, fertile).
          Stigmas commissural . Ovules in two rows.

e 2.   *Lunaria* (latiseptal silicula). G 4 (two small, flat, valve, sterile;
          two semi-solid, boat-shaped, fertile).

e 3.   *Capsella bursa-pastoris* (angustiseptal silicula). G 4 (two small, boat-
          shaped, sterile, valve; two semi-solid, flat, fertile).

e 4. *Capsella heegeri* (cylindrical silicula). G 4 (two small, shallow boat-shaped, sterile, valve, wider than in *C. Bursa-pastoris*; two semi-solid, shallow, boat-shaped, fertile, narrower than in *C. Bursa-pastoris*).

e 5. *Bunias* (four-sided, four-angled silicula). G 4 (two flat, valve or semi-solid, sterile; two flat, semi-solid, fertile).

e 6. *Biscutella* (silicula). G 4 (two closed, valve, fertile; two solid, sterile).

e 7. *Tetrapoma* (short siliqua). G 4 + 4 (four orthogonal, valve, sterile; four diagonal, solid, fertile).

e 8. *Capsella viguieri* (four-winged silicula). G 4 + 4 + 4 (four small valve (or solid), sterile, four semi-solid, fertile in the lower region, and four fertile in the upper region).

STUDIES IN THE PHYSIOLOGY OF CAMBIAL ACTIVITY

I. CONTRASTED TYPES OF CAMBIAL ACTIVITY[1]

By J. H. PRIESTLEY

(With 2 figures in the text)

CONTENTS

INTRODUCTION

As a result of the studies of meristematic activity in the higher plant that have been in progress in the botanical laboratories at Leeds for some years past (23, 24), the activities of the cambium have been under observation for some time, but, with one slight exception (22), the results of this work have not been placed upon record, although certain published studies upon vegetative propagation have dealt indirectly with cambial activity. It is proposed, therefore, in the present series of papers, to present the results of some of these anatomical and experimental studies, but in view of the manner in which the work has developed, a preliminary statement seems necessary as to the form these papers will take.

During recent years, especially, a very large amount of data has accumulated as to cambial activity. These data, which can to some extent be confirmed and, in part, extended by the Leeds observations, make a definite contribution to our knowledge of this tissue as supplied to us by such pioneers of the study of plant anatomy as Sanio and Th. Hartig, etc., in the nineteenth century. In considering these data, however, from the standpoint from which meristematic tissues have come to be regarded in this laboratory, the conviction has grown that they are, at present, in many respects

misinterpreted and that their significance in relation to the general biology of the living tree has to a large extent been missed. In these papers, therefore, it is very little a question of placing upon record new observations, but far more of critically reviewing the facts as to cambial activity and in many cases attempting their re-interpretation. Where possible, then, these papers will be based upon the published literature dealing with the cambium and additional data, resulting from the laboratory study of the subject, will only be drawn upon as needed.

In taking this course, the work of the writer is materially aided by the many critical reviews of the subject that have appeared in recent years. He is especially indebted to the series of papers by Irving W. Bailey (1, 2, 3, 4, 5, 6, 7, 8, 9), whom he has also to thank for many interesting private communications received during the course of the preparation of these papers. A very valuable historical analysis of the growth of our knowledge of the cambium will also be found in the recent paper by Beijer (10).

In this first paper, use will be made of the data supplied by Bailey in contrasting cambial activity in the Conifer, or soft-wood tree, and the Dicotyledon, or hard-wood tree. It will become increasingly evident as this series of papers proceeds that the differences between these two types of cambial activity are very fundamental in nature. The significance of these differences receives considerable elucidation when examined from the standpoint from which the meristematic activities of the apical growing point have recently been considered (24).

Later papers to appear in this series will include:

II. The concept of gliding growth.
III. The seasonal activity of the cambium.
IV. The movement of water in the tree in relation to cambial activity.
V. The movement of solutes in the tree in relation to cambial activity.

With some of these papers the names of other members of the Botany Department will be associated. The work as a whole has arisen out of a series of investigations carried out in association with members of the staff and with honours and graduate students. The general form in which the results can now be presented owes much to discussion with a succession of honours classes. Considerable advantage has also been derived from the close touch that has been

maintained by the Department with the Horticultural Research Stations at Long Ashton and East Malling, and in particular with the observations upon the growing fruit tree made by Dr T. Swarbrick at Long Ashton and Dr R. C. Knight at East Malling.

MERISTEM CELL, PROCAMBIUM CELL AND CAMBIUM CELL

It is the essential thesis of this series of papers that the cambium cell is potentially equivalent to a cell of the apical meristem, and that its different form and behaviour are the result of the different conditions under which it is placed in the tissues. It is not sufficiently recognised as a rule that there is a very gradual and continuous change from the type of cell characteristic of the apical meristem to that characteristic of the cambium. If longitudinal sections are made of the young shoot of either Conifer or Dicotyledon, from materials which have been suitably fixed before cutting and staining, the procambial cells are seen to have the same general cytological characteristics as the cells of the apical meristem. In particular, they are densely filled with cytoplasm containing a spherical nucleus, but no other very conspicuous cell inclusions. As the cells become more compressed radially, the nucleus is held between the two walls that thus close upon it and alters its shape just as a drop of oil gripped between two parallel glass plates.

The meristem cells at the apex were seen to be in close and continuous contact with each other on all wall surfaces as the result of the constant growth and expansion of the semi-liquid protoplasmic contents against a relatively plastic wall. The procambial cells are similarly in close and continuous contact with no intercellular spaces between them, but in this case the cells are much flattened in a radial direction, being carried outwards by the expansion of the vacuolating pith and held firmly against the vacuolating cortex (23). This compression is accompanied by longitudinal extension because the procambial cells have space to extend in a longitudinal direction in the young internode in which the vacuolating, dividing cells of the pith and cortex repeatedly divide by transverse walls and continue to elongate in a longitudinal direction. Within the procambial strand certain cells are characterised, at a very early date, by their repeated division by longitudinal tangential walls. These cells are the cambial initials; they are in all respects like compressed and elongated meristematic cells in which the outstanding characteristic is this frequent repetition of a type of division which violates Errera's law that the new wall should form in a plane of minimal area. A reason for this

remarkable characteristic has previously been suggested(23); it is this type of division which gives rise inwards to the secondary xylem, outwards to the secondary phloem, so that both these tissues frequently stretch in regular radial order from the cambium initials. (The controversy as to whether there is one or more initials will not be entered into here; its history is very fully given by Beijer(10) and in the literature there cited. Our own point of view will emerge in the course of the general discussion of cambial activity.) After the shoot internode has once attained its full length behind the growing point with the full extension of the vacuolated parenchymatous tissue(24), all further meristematic activity in this region of the axis is usually intercalary cambial activity and the shoot only increases in radial girth. In the axis of the tree this process continues in successive growing seasons for many years and is the pre-occupation of the forester. Clearly it is a process of which the fullest understanding is desirable, and no apology should be necessary for this attempt to submit the data dealing with this fundamental growth process to a re-examination from a standpoint which is to some extent a new one.

It is suggested, then, that the cambium initials are radially compressed meristem cells. The latter were described, at the shoot apex, as imperfect 12- or 14-sided figures, such as, in symmetrical systems, meeting at angles of 120°, can be shown to partition space homogeneously. In section such cells often appear hexagonal, and it is striking how frequently the radially compressed cells of the cambium of the Dicotyledon retain the hexagonal form, whether examined in transverse, radial longitudinal or tangential longitudinal section (Kleinmann(14), Beijer(10)). In the Conifer these cambium cells are still more elongated until they rather resemble compressed and flattened threads with a greater tangential diameter near the centre of the elongated structure. Bailey terms these elongated cambium initials "fusiform initials," and this term will often be used, in a general sense, in this series of papers, to denote the elongated, plastic meristematic cell which by repeated tangential divisions gives rise to the secondary xylem and phloem. These cells are thus placed in contrast with the less compressed and flattened "ray initials," which are found side by side with the fusiform initials in the cambium ring. These ray initials are not so compressed, presumably because they have a higher internal osmotic pressure and are equivalent rather to the vacuolating, dividing cells, which similarly, in the shoot apex, are found side by side with the plastic meristematic cells from which they have been derived(24). A more detailed consideration

of these two types of cambium cell will now follow, in reference to the two types of cambial activity, characteristic respectively of Conifer and Dicotyledon.

CAMBIAL ACTIVITY IN THE CONIFER

During the increase in girth of the stem of a Conifer, various changes may account for the increase in the ring of meristematic tissue. Two types of cell are present from the very beginning of the ring, the fusiform initials with pointed ends, which by successive tangential divisions give rise to new elements of xylem and phloem, and the short almost iso-diametric cells, the (medullary) ray initials, which give rise to the radially elongated cells of the ray. The increase in the periphery of the ring may be due to an increase in number of the cells in the ring or to an increase of the tangential diameter of the cells present. The following table, which gives the result of a comparison made by Bailey of the cambium in one-year-old and sixty-year-old stems of *Pinus strobus* L. ((9), *loc. cit.* p. 501), will permit some conclusions on this point.

TABLE I

One-year-old stem

Radius of woody cylinder	2,000	microns
Circumference of cambium	12,566	,,
Average length of fusiform initials	870	,,
Average tangential diameter of fusiform initials	16	,,
Average tangential diameter of ray initials	14	,,
Number of fusiform initials in cross-section of the stem	724	
Number of ray initials in cross-section of the stem	70	

Sixty-year-old stem

Radius of woody cylinder	200,000	microns
Circumference of cambium	1,256,640	,,
Average length of fusiform initials	4,000	,,
Average tangential diameter of fusiform initials	42	,,
Average tangential diameter of ray initials	17	,,
Number of fusiform initials in cross-section of the stem	23,100	
Number of ray initials in cross-section of the stem	8,796	

From this table it will be seen that the increase in peripheral extension of the ring over this period of 60 years is some 100-fold. The portion of the periphery occupied by the fusiform initials has only increased some 60-fold, as the number of these cells has increased about 30-fold and their tangential diameter, 42/16, i.e. from two to three times. The fusiform initials have therefore not

quite kept pace with the increase in girth. The ray initials, on the other hand, have increased approximately 125-fold, and as at the same time they have increased some 20 per cent. in tangential extension, their total peripheral increase has been some 150-fold. As they occupied originally some 7–8 per cent. of the periphery and now occupy about 12 per cent. (149,522 microns out of 1,256,640), this proportionately greater rate of extension of the medullary ray initials accounts for the amount to which the extension of the periphery, as a whole, is greater than the tangential extension of the region occupied by the fusiform initials.

Nägeli[20] was one of the first to visualise the significance of this peripheral increase of the cambium ring. To explain it he constructed a theoretical scheme of cell multiplication, in which the cells of the ring increased in number by radial longitudinal divisions. There is now, however, a consensus of opinion that no such divisions are ever met with in the fusiform initials of the Conifer, which divide only in two planes: (1) by tangential divisions which add new elements to both xylem and phloem, and (2) approximately transverse divisions which increase the number of cells in the cambium ring itself. The short transverse walls formed in these latter divisions are almost immediately inclined obliquely, and the pointed ends of the upper and lower cell thus separated begin to move past one another, the cells becoming continually more pointed. Thus the number of cells in a cross-section is increased as a result of this type of division and subsequent relative movement. This explains the fusiform shape of the cambial initial, and also the lack of any appearance of serial order in the cells of the cambium when they are regarded in tangential longitudinal section. This type of growth is better understood when the general changes in cell shape and size in the cambium ring are considered in the light of the composition of these living and growing cambial elements.

The fusiform initials

The fusiform cambium initials seem to be meristematic cells as this type of cell has been defined in previous papers[23, 24]. In their elongated form these cells do not remain of so small a mass as was characteristic of the iso-diametric cells at the apex. Bailey emphasises their relatively great mass, in which, however, the nucleus remains about the same size as the nucleus in the cell of the apical meristem, so that the ratio of nucleus to cytoplasm is very considerably lessened[4, 6, 8]. The writer has previously pointed out[23, 24]

that the protoplasm of such relatively non-vacuolated meristematic
cells is probably all engaged in the construction of protoplasm, and
that under these circumstances the important balance to maintain
is not that of mass of nucleus to cytoplasm but of cell surface to mass.
When, therefore, these cells undergo elongation under pressure, in-
crease in mass is accompanied by a proportional increase in length
and therefore of surface, so that the fusiform initial may have a
much greater mass in proportion to the protoplast of the apical
meristem, and yet remain an efficient unit for the manufacture of
protoplasm.

From this standpoint, the change in shape from the cell of the
apical meristem to the fusiform initial is a change resulting from the
gradual increase in radial pressure upon a plastic meristematic cell.
The radial pressure in the procambial ring resulted from the vacuola-
tion of pith and cortex. In the woody stem this pressure is replaced
by that of the outward expansion of the differentiating xylem and
the resistance to this expansion of the tissues outside the cambium.

As a cell is separated from the inside surface of the cambium ring,
and becomes part of the xylem, it vacuolates and increases in volume
considerably. In longitudinal and tangential directions the increase
in dimension is slight, but there is often a very marked increase
(two to five times) in a radial direction. In the Conifer each radially
expanding tracheid lies between an already lignified xylem element
within and the plastic cambium without. The full pressure of this
radial expansion is therefore borne by the cambium, which is thus
always under pressure and *a pressure which grows with increase in
cambial activity*. During the first 60 years of a tree like *Pinus strobus*,
this cambial activity is usually increasing and with it, therefore, the
radial pressure on this plastic layer. This increased pressure is
reflected in the increased length and tangential extension of the
fusiform initials which in this period, as Table I shows, become five
times as long and nearly three times as wide tangentially. The increase
in length and breadth of the fusiform initial is not accompanied by
an equivalent decrease in radial thickness, so that it means an in-
crease in the mass of these initials. The change in size and form of
these cells is naturally associated with considerable mutual adjust-
ments between the cells, especially following upon the occasional
transverse divisions: divisions which are in consonance with Errera's
law, the new walls being of minimal area. This mutual readjustment
is usually stated to occur by "sliding growth," the apex of one
fusiform initial being regarded as pushing in between two other

initials, the walls sliding over one another. This is an interpretation
of the observed transition from two cells end to end; with a nearly
transverse partition between, to the final form of two very pointed
initials overlapping one another for a considerable distance (Klin-
ken (15), Bailey (7), *loc. cit.* p. 365). But these changes may occur quite
simply in another way in which relative shifting of the adjacent
walls is avoided. Actual sliding growth would mean that these two
plastic units, with their thin walls interpenetrated by protoplasmic
contacts, should move past one another, thus shearing all these pro-
toplasmic connections. These would then have to be built up afresh
in the radial walls of the differentiating elements in which the pits
are undoubtedly built around protoplasmic connections and are
exactly opposite one another in the opposed radial walls of two neigh-
bouring cells. Such a reconstruction of protoplasmic connections is
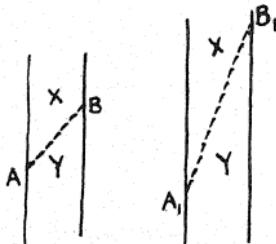
Fig. 1. For description see text.

difficult to believe in. In actual fact, the changes in shape involved
do not require any such sliding movement of individual fusiform
units past one another. The cross wall AB in Fig. 1 could reach the
position A_1B_1 simply by gradual extension of the *joint* wall between
the two cells, and without any relative movement of the separate
walls of the two elements X and Y, so that any protoplasmic con-
nections originally facing one another through the wall still remain
in the same relative position. But the problems raised by this ex-
planation alternative to sliding growth are so numerous and im-
portant, that they must be put on one side for the moment. They
will be examined in the second paper in this series.

These changes in cell shape, following upon a transverse division
of the fusiform initial, presumably take place gradually with the
growth of the cell. And this growth in size of the cell, interrupted
continually by the frequent tangential division of the initial, is a
very gradual process. Examine the data supplied by Bailey for

Pinus strobus from this point of view. In 60 years the fusiform initials have grown in number from 724 to more than 23,100, but less than 32,000 (the larger number allows for the fact that certain fusiform initials have been converted, in whole or in part, into ray initials). During this period the fusiform initials have increased in length about five times, so that only one-fifth of this number (32,000) is the result of cell divisions, the rest is due to the increased length of the initials. Thus, during these 60 years, 724 cells have increased to some 7000. As each new fusiform initial grows and divides in its turn, a succession of four transverse divisions in the original 724 initials and their progeny (700 → 1400 → 2800 → 5600 → 11,200) during this period of time would account therefore for all the cells now found in the periphery. This works out at a division once in about 15 years in any individual initial!

Bailey finds that the tracheids differentiated from these fusiform initials are never much longer than the initials: at most they may be some 5–10 per cent. longer. A number of measurements of tracheid length in the different annual rings of Conifers are available, and from these conclusions can be drawn as to the changes in length of the fusiform initials. On the whole, Sanio's original conclusion holds good (25), that tracheid length increases fairly rapidly over a period of years and then remains comparatively constant, though Bailey's numerous measurements show that the subsequent fluctuations are by no means negligible (1, 2, 3, 7). The same change in length will then hold good for the cambium initials, where it is possibly connected with the increasing pressure upon the plastic cambium. This point, however, will require much closer examination. Vigorous radial growth means rapid tangential division of the fusiform initials. If this results in the postponement of transverse division of these initials it will certainly be associated with longer initials, but if a vigorous growth of the cambium involves a more frequent transverse division a wider annual ring may be correlated with a shorter fusiform initial.

In any case the progressive increase in length of the fusiform initial over a period of 50–60 years, or even longer, which is recorded by Bailey, suggests an interesting correlation with the vigour of growth of the tree if not, necessarily, with the width of the annual increment of wood added each year. The longest tracheids, and therefore presumably the longest fusiform initials, are not found at the base but some distance up the trunk, and from this region the length of the tracheids within the same annual ring diminishes both

downwards towards the base of the trunk and upwards towards the growing apex. Bailey found the maximum average tracheid length further from the base of the tree, as the annual rings under examination were progressively further from the centre of the stem. This again is suggestive, because, as is pointed out in a later paper, there is reason to think that cambial growth, as the tree grows older, is often more vigorous in a region which is progressively further removed from the base of the stem.

The ray initials

It is obvious from the figures previously given that ray initials are continually forming in the cambium at the expense of the fusiform initials. Such a change in a fusiform initial means a cessation of its longitudinal extension, a succession of transverse divisions and the formation of a file of nearly iso-diametric cells, because, as the transverse divisions occur, the new cells are extending in a radial direction. The change in radial dimension suggests at once that the change is accompanied by an increasing vacuolation, so that the new cells are more resistant to the external pressure that compresses the plastic fusiform initials. Thus whilst the ray initials have a radial dimension that is usually four or five times as great as that of the fusiform initial, from Table I it will be seen that the latter extend tangentially under compression from 16 to 42 microns during the first 60 years in *Pinus strobus*, and the ray initials in the same time only extend from 14 to 17 microns. In the cambial ring, in fact, the ray initials contrast in their behaviour with the fusiform initials just as the vacuolating dividing cells contrast with the meristem cells in the shoot apex[24]. So long as the rays are uniseriate, this type of cell division may not give rise to intercellular spaces, as the plastic fusiform initials lie on the flanks of the files of ray cells and are closely pressed against their radial walls. Nevertheless close examination of tangential sections shows that small spaces are often formed at the corners of contact between the ray cells and the radial walls of the adjacent fusiform initials. These spaces remain very small, but in the multiseriate rays of the Dicotyledon they will be found to be very much more developed and of great physiological importance.

In the series of transverse divisions by which it gives rise to ray initials, the vacuolating fusiform initial readjusts the ratio of nucleus to protoplasm in favour of the nucleus. Evidently during this series of divisions nuclear material is mainly constructed and afterwards, as has been suggested for other vacuolating dividing

cells, the synthesis of protoplasm prior to subsequent divisions is probably carried out only by the nucleus and a fairly definite ratio of mass of nucleus to cytoplasm retained in the dividing cells (24). The ray initials do not divide so frequently as the fusiform initials, nevertheless the radial growth of the tissues formed by the tangential divisions of the ray initials keeps up with the radial growth of the tissues cut off by the more frequent divisions of the fusiform initials, because the cells of the ray have proportionately greater radial dimensions.

In the shoot apex, another characteristic of division in the vacuolating cell was that the walls continued to thicken after formation, so that it was possible to distinguish walls of different age and thus determine groups of cells that had originally sprung from one cell. Along the radial file of a ray this has usually not been found possible, though in a tangential longitudinal section in the region of the cambium the walls of the ray cells sometimes appear thicker than those of the fusiform initials. Probably the cells do not divide again after they have been displaced from the immediate neighbourhood of the cambium ring. Sanio (25) and Mischke (18) have described such divisions as occurring in the products of tangential division from the fusiform initials, in both young phloem and xylem elements. Mischke saw this best in an actively growing specimen of *Pinus sylvestris*. In this case the newly differentiated vascular elements seem to have continued to divide by tangential walls as they vacuolated and commenced to synthesise carbohydrate rather than protein.

Thus in the activities of the vascular cambium leading to intercalary growth, as in the growth of the apex of the shoot, two types of dividing cell have been found, the meristematic cell and the vacuolating dividing cell. Two lines of evidence suggest the presence of the meristematic cell in the cambium ring: (1) in microtome studies of fixed material there is no distinction between the cytology of the cells of the apical meristem, of the procambial strand and the young fusiform initial; (2) in the older cambium the changes in size and form of these fusiform initials are best understood on the assumption that they are cells that are deformed under external pressure and fail to develop an internal hydrostatic pressure against a resistant elastic envelope like a normal vacuolating cell. Similarly the different behaviour of the ray initial, with its different changes of form and size, are best understood on the assumption that it is a vacuolating dividing cell.

CAMBIAL ACTIVITY IN THE DICOTYLEDON

Whilst most of the Conifers have a woody shoot which, whether bush or tree, is built up in very much the same way, the shoot of the Dicotyledon shows an extraordinarily wide range of forms, and it is not to be expected that throughout this great group the phenomena of cambial growth will be proceeding on uniform lines. It would be premature to attempt a formal characterisation of this range of cambial types, but, in the light of Bailey's work, some of the main tendencies among the Dicotyledons can be detected, and it is thus possible to correlate in a very interesting manner the progress of vascular differentiation with the changes in the cambium.

Some genera of the southern hemisphere, notably *Drimys* and *Trochodendron*, are without true vessels, and in these types the cambium, both in the length of the fusiform initials and in the types of cell division found in the cambium, conforms strictly to the Conifer type. With the development of vessels there seems to be shortening of the fusiform initial, which, in particular, ceases to extend so much in length with the increasing age of the cambium. Bailey thus divides the Dicotyledons with vessels into three groups, as follows ((9), *loc. cit.* pp. 506–507):

(1) Cambial initials of average length about 890 microns, vascular tissues not highly differentiated.

(2) Cambial initials of average length about 410 microns, vascular tissues highly specialised.

(3) Cambial initials of average length about 250 microns, vascular tissues highly specialised, cambium "stratified."

In this third group a new type of cambium is indicated, but throughout the series there is an interesting parallel change in length of cambium initial and type of vascular differentiation. Along with the development of the vessel, there is found a wider range of tissue types in the wood, so that the appearance of the Dicotyledon wood is much more varied and irregular, an irregularity which extends to the order of development of the differentiating elements. These elements are of two general types, on the one hand the wide water-conducting vessel segments and tracheids, which are never much longer than the cambium elements from which they have arisen, but have undergone considerable expansion horizontally, and on the other hand the fibres, fibre-tracheids and parenchyma, which are narrow elements, but which in the case of the fibres are often several times as long as the cambium initials from which they have arisen.

The appearance of these two types of vascular element simultaneously, in differentiating wood which is less regular in development, at once suggests that the vessels and large tracheids have undergone early vacuolation. They are thus able to expand horizontally by compressing the surrounding plastic unvacuolated elements, which as a result are much elongated but compressed laterally. Often the latter are so compressed in a tangential direction that they have finally a tangential dimension less than half that of the cambial initial from which they were originally cut off. This diminished tangential breadth is not likely to have resulted from a later radial longitudinal division, because, if it had, the narrow elements would always occur in pairs, which is not the case. These compressed and much elongated elements differentiate and lignify later than the tracheal elements, and form the fibres or files of xylem parenchyma. They are sometimes regarded as growing past one another during development by a process of gliding growth, but their method of growth will be examined more closely when details of their wall structure are under examination.

In the group of Dicotyledonous woods with a less highly developed vascular system the vessel segments as they vacuolate also increase slightly in length, but in the more highly specialised groups the vessel segments or tracheids often expand so readily laterally that the top and bottom of the vacuolating cell are drawn together a little as the cell expands in girth, and the differentiated element is a little shorter than the cambium initial. In the Conifer, the pressure which caused the gradual increase in length of the fusiform cambium initial was the radial outward pressure of the differentiating tracheids. These expanded almost entirely in a radial direction and differentiated in a regular centrifugal order so that the full pressure of this expansion was exerted upon the cambium. In the type of differentiation just described for the Dicotyledon, the pressure of the vacuolating elements as they differentiate in irregular order is chiefly taken up by the remaining undifferentiated, unvacuolated plastic xylem elements, so that whilst these are elongated under pressure the cambium initials are under much less pressure, and this pressure may not increase at all with the growth of the plant. The result is a relatively short cambial initial, which increases very little in length during the life of the plant. The length and shape of the fibres in the wood contrasted with that of the cambium initials from which they arise is clear evidence that the horizontal expansion of the xylem vessel or tracheid has been achieved at the expense of lateral com-

pression and longitudinal extension of the surrounding elements. The contents of these surrounding elements are, however, incompressible and they have not much, if any, vacuolar sap to lose. It therefore remains to be shown how the compression of the neighbouring fibre initials can be brought about without, as a result, producing an exactly similar radial compression upon the cambium. The point cannot be finally elucidated until the method in which these fibre initials alter their form is considered in detail, and these facts in their turn are connected with the manner in which the activity of the cambium varies with the season.

Observations of the wood as it develops in the spring, when lignification lags far behind vacuolation (Kostytschew[16], [17])), make it very clear that the vessel segments and wide tracheids are the first elements to vacuolate, and subsequently the first to lignify. It will be noted that the tendency that has been thus traced in the wood of the Dicotyledon, with increasing vascular specialisation, is a growing tendency for the lignified vascular elements to be interspersed amongst elements that, at first at least, are slower to lignify. If these elements *remain* unlignified, then the secondary tissues of the shoot show one characteristic tendency of the Dicotyledon, the trend towards the herbaceous habit.

Another characteristic feature of the Dicotyledon is the greater development of medullary rays. In the figures of the cambium ring in *Pinus strobus*, from 8 to 12 per cent. of the cells in the ring consisted of medullary ray initials, but in the Dicotyledon these often compose more than 50 per cent. of the ring. These cells are again dividing vacuolated cells, and as the pressure upon them, preventing their natural expansion, is much less, and as the rays are usually multiseriate, intercellular spaces are almost invariably developed between the cells, which often also have thicker cellulose walls. These intercellular spaces may not always be filled with air, but many years ago Klebahn[13] pointed out that air could be driven along the wood, in a shoot which was ringed through the phloem, and that if the end of the shoot were stopped up and dipped under water, the air could be seen to bubble out laterally, moving out from the wood through the ray and then through the lenticel which is usually to be found opposite the end of a ray. A very small head of mercury was sufficient to drive the air in this way along the wood and the rays, and thus through the cambium, in the stems of *Berberis*, *Vitis*, *Lonicera* and *Clematis*.

The stratified cambium of Bailey corresponds to the "palisade"

cambium of Von Höhnel[11], and is sometimes known as "etagen-cambium." The name is given because of the characteristic appearance of the cambium in tangential longitudinal section (Fig. 2). The cells lie in regular series stretching in a horizontal direction, so that they are evidently related to one another as the result of successive radial longitudinal divisions. Although Von Höhnel and Neeff[21] suggested that this appearance might be the indirect result of sliding growth following upon transverse division, Bailey, Kleinmann[14] and Beijer[10] have all seen radial divisions in these stratified cambia, and there is little doubt that this is the way in which peripheral increase takes place in this type of cambium. There is no need, however, to argue, as Kleinmann has done, that transverse divisions only take place in a cambium so long as the axis is extending in length,
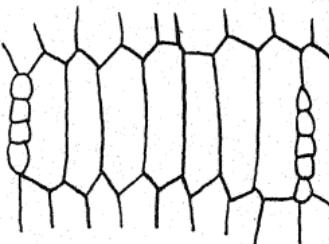
Fig. 2. Stratified cambium in tangential longitudinal section in *Herminiera elaphroxylon* (after Beijer).

and that subsequently all divisions are radial longitudinal. Kleinmann found transverse divisions in the growing shoots of *Sambucus*, *Aesculus*, *Phaseolus* and *Phytolacca* only during elongation, but these are all Dicotyledons with specialised vascular systems; there is no doubt that transverse divisions without any radial longitudinal persist throughout the life of the cambium of the Conifer. They also probably occur in Dicotyledons without vessels and many other less specialised Dicotyledons (Neeff[21]). On the other hand, it is not so easy to decide whether radial longitudinal divisions are restricted to Dicotyledons with "stratified" cambia. In a census of Javanese woods, Moll and Janssonius[19] found that some 5 per cent. had a stratified cambium. Beijer showed, by applying Klinken's method[15] of serial tangential sections to the wood of the root of *Herminiera elaphroxylon*, that the first cambial initials of the root were not in regular horizontal rows, so that the original divisions in the initials, during elongation of the root, had probably been transverse. After

this very early stage all subsequent divisions that added to the number of cells in the ring were radial longitudinal. Klinken's method cannot be applied to wood in which the arrangement of the elements, as laid down by the cambium, is subsequently destroyed by the vertical extension of some of these elements, as is the case in the vast majority of the Dicotyledons, in which the radial and tangential expansion of the vessel segments and the wider tracheids has brought about the elongation of the narrow fibres. Actual observations of cell division in the cambium are very few and practically restricted to Bailey and Kleinmann. In Dicotyledons with vessels and fibres longer than the cambium initials but without a stratified cambium, it must therefore be left for further observations to show whether divisions in the cambium are usually transverse or radial longitudinal. Radial longitudinal divisions need not necessarily give a stratified cambium, because the subsequent differentiation of the wide vessels and tracheids may take place so close to the cambium that the cambium cells may be amongst the plastic elements which undergo vertical elongation as the result of the sideways pressure exerted by the vacuolating elements. Thus Beijer points out that when these cambium initials are not much longer than broad, very little vertical elongation quickly distorts the horizontal series as seen in tangential longitudinal section. He cites as an example the cambium in a species of *Alstonia*.

CONCLUSION AND SUMMARY

It appears, then, that when the same arguments as to the conditions governing cell growth and division, as were applied in a previous paper [24] to the shoot apex, are applied to the cambium, very obvious correlations come to light between the contrasted form and mode of growth of the cambial elements in the Conifer and Dicotyledon, and the different types of vascular differentiation in these two groups. In the Conifer differentiation is regular and centrifugal in the uniform tissue released from the inside of the cambium, and all the radial pressure resulting from the resultant expansion of the vacuolating and lignifying tracheids is directed against the sheet of plastic elements in the cambial cylinder, the shape of the plastic fusiform initials being thus determined. In the Dicotyledon, on the other hand, the differentiation of individual elements in the developing xylem is sporadic and localised, so that here and there future tracheal elements vacuolate and expand horizontally, deforming neighbouring plastic elements, which thus assume the form of the future fibres

and files of wood parenchyma. For reasons that will become clear later, the pressure upon the plastic elements in the cambium ring, due to the increasing production of xylem, is not reflected in an increasing elongation of the fusiform cambium initials as it is in the Conifer. In the more specialised Dicotyledons a new type of cell multiplication, by radial longitudinal septation, also appears in the cambium and leads to the production of the "stratified" type of cambium. This is a type of cell division not conforming to Errera's "law," but at present it is not examined further. The tangential longitudinal division, which is most characteristic of the fusiform initial, is equally contrary to Errera's law. This type of division has been discussed previously(23), and the radial longitudinal divisions may be a somewhat similar phenomenon.

The factors governing cambial division and the plane of these divisions will not be examined further, however, at this stage of the investigation. The present paper has simply brought out the correlation between the form and structure of the living cambial elements and the type of xylem elements to which they give rise. In the next paper the conception of "gliding growth" will be more critically examined, and in the third paper the periodic nature of cambial activity will be dealt with. Before any attempt is made to identify the factors governing cambial activity, it is necessary to know the facts as to its commencement, maintenance and cessation in different regions of the cambial cylinder at different seasons of the year.

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ON THE PREPARATION OF CELLULOID
TRANSFERS FROM ROCKS CONTAINING
FOSSIL PLANTS

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IN 1928 Walton(1) described a method for the preparation of celluloid transfers of fossil plants. Experiments with this method have led to the adoption of changes in technique by which the preparation of slides has been facilitated from coal balls from the Lower Yorkian, from silicified material from Pettycur, and from blocks of the Rhynie deposit.

Surfaces to be etched are smoothed by rubbing them down with a thin paste of water and carborundum powder, on a sheet of thick glass. For preliminary smoothing, a coarse powder of grade no. 90 is used, followed by a finer powder of grade no. 220, and this by ordinary knife powder on a third sheet. The piece of rock is well washed between treatment with each grade of powder, to prevent contamination of the finer grinding pastes with coarser particles. Calcareous rock is often sufficiently smoothed by the second grade of powder; a finish with knife powder is necessary for clean results with siliceous rock, and improves preparations from coal balls. After material has been treated with acid, it is seldom necessary to grind with the coarsest powder, but it is always necessary to take the surface down to a level below that reached by the etching acid.

Coal balls are sufficiently etched by immersing the smoothed face in 2 per cent. hydrochloric acid for 10 minutes: the siliceous material gives good results after 6 to 8 minutes in strong commercial hydrofluoric acid; very thin sections may be obtained by shortening the time of exposure. The block of stone should be inverted in the acid, for when acid is applied to an uninverted surface, particles of undissolved mineral remain in the interstices of the petrifaction and spoil the preparation. The blocks may be supported in the acid by resting them on pieces of match stick lying on the bottom of the vessel. As etching is always much less where supports touch the prepared surface, it is necessary to ensure that parts of the surface containing good material are freely exposed to the acid.

After etching, the blocks are washed for some minutes in running water; if they are still acid, they may be rinsed in a weak solution of sodium carbonate, or exposed for a short time to gaseous ammonia. Finally, they are dried by gentle heating.

Dry blocks are supported with the etched face in an approximately horizontal position, wetted with sufficient absolute alcohol to form a layer over the flat surface, and then covered with a solution of celluloid. A useful solution for this purpose is made by soaking pieces of celluloid in a mixture of equal parts of absolute alcohol and ethyl ether; waste celluloid from the cinematograph industry serves well. The solution should be about as viscous as pure glycerine, and is best prepared by making a thick solution, and diluting with the solvent to the consistency required. It must be free from water, and, when used, should contain no bubbles.

Enough solution is poured on the block to form a layer about 2 mm. thick all over the prepared surface. The layer soon skins over, and, almost always, bubbles appear in a minute or so. They may often be burst by allowing the fumes from a bottle of ether to fall upon the skin; it is sometimes possible, by this simple method, to get rid of all the bubbles. Obstinate cases may be dealt with by wetting the skin with a drop or two of absolute alcohol, and then either allowing fumes of ether to stream over the surface, or applying a drop or two of liquid ether. It is usually sufficient to remove the bubbles only from the areas containing good material, and from these regions clearance should be complete, for, as the film dries, the bubbles flatten against the fossil remains and usually damage them.

The solution of celluloid dries to a thin, tough film, a fraction of a millimetre in thickness, in 2 to 3 hours, and can then be removed; it is best left for 6 hours at the least. The point of a sharp knife is now inserted at the edge of the block, and pushed along between the celluloid and the etched surface. This detaches the edge of the film, and the middle usually leaves the stone without further manipulation, or needs but a slight pull to detach it. Separation appears to be less ready from siliceous rock than from coal balls; in difficult cases the process may be assisted by the cautious insertion of a knife blade between film and stone.

As a rule, the side of the transfer next to the stone is rough when it is taken off; it seems that the solution of celluloid does not penetrate quite to the general depth reached by the acid, and that a thin layer of loosened material is torn away with the film. This should be removed. Sometimes gentle rubbing under water between finger and

thumb is adequate, but cleaner results are obtained when the surface is rubbed carefully, with very slight pressure and a circular motion, on the slightly roughened surface of the glass used with the knife powder. After three or four rubs the transfer is washed and inspected with a lens; the treatment is repeated as necessary until the under side of the film is clean and the sharp outlines of the plant remains can be seen inside the celluloid. All the lower surface need not be rubbed smooth; the treatment may be limited to areas containing useful material.

The transfer is now well washed in water, dried with blotting paper, and smeared evenly and liberally with Mayer's egg albumen[1]. A slide is heated in the flame until it is just too hot to be touched with comfort, but not so hot as to cause the albumen to boil, the film is quickly applied to it, and well thumbed down. If the film is curved, some flattening will result from the heating, and the processes of flattening and adhesion are aided by the addition of a few drops of absolute alcohol. By these means films up to 1 mm. in thickness may be successfully mounted, though thin films are preferable. When it is clear that the transfer is firmly attached to the slide, the whole is placed in a nearly vertical position in a tube containing a mixture of equal parts of absolute alcohol and ether. The celluloid swells and dissolves, leaving the fossil transfer on the slide. When solution is complete, the preparation is finished as a balsam mount in the usual way.

The authors are indebted to Professor W. T. Gordon for the loan of blocks of siliceous material.

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[1] White of egg, 50 c.c.; pure glycerine, 50 c.c.; sodium salicylate, 1 grm.

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A METHOD FOR DEMONSTRATING THE SHAPE OF MERISTEMATIC CELLS IN PLANTS

By R. GANE

PRIESTLEY(1) has given his reasons for believing that cells in apical meristems and in the cambium have plastic contents and a non-rigid wall, and considers that the shape of these cells is determined by the pressure of surrounding cells.

The simplest representation of such a system appears to be that of a compact mass of approximately uniform soap bubbles. Such a system has been considered at length by D'Arcy Thompson in his book *Growth and Form*. This method does not lend itself as a convenient demonstration for class use, and the following method was devised to meet the teaching needs in the Botany Department at Leeds University.

Spheres of about 1 cm. diameter, made from well-handled plasticine, are dusted with powdered talc (French chalk), by rolling them in a dish well dusted with the talc. A cylindrical container, such as the metal cup of a thermos flask, is well dusted inside with the talc, the pellets put in and gently shaken down. A glass stopper, which will slide easily in the cup, is also dusted with the talc and then rammed down into the cup. The pellets are deformed by the pressure and are packed tightly together. After this treatment the pellets may be separated very easily from one another and are found to be irregular plane-sided solids having from twelve to fourteen faces, and are very similar in form to the macerated meristematic cells of *Vica Faba* examined by Tupper-Carey and Priestley(3). If a permanent copy is required, this may be obtained in plaster of Paris by pouring a little thin plaster into the cup after the first layer of solids has been removed; or alternatively, by using putty instead of plasticine.

By regulation of the amount of chalk used, one can cause the pellets to adhere together fairly well but not to the cup, so that they may be removed from the cup as a mass. Using a knife dusted with chalk, and exercising a little care, the mass may be cut in any direction without disturbing the packing. Such sections are not unlike those made longitudinally through part of the apical meristem of the higher plants.

It is obvious that the method described above will not give regular solids, since it does not involve a systematic packing of the spheres prior to deformation. Using a rectangular container, the spheres were packed regularly in three different ways and then subjected to pressure. It is interesting, in that the case where "closest packing" is used, that is where one sphere is surrounded by and touches twelve others, a solid figure is obtained not with twelve faces but with fourteen, reminiscent of the well-known tetrakaidecahedron of Kelvin[2].

Another modification of this method is to pack the pellets to a thickness of three layers on a strong glass or metal plate, then cover with another plate of the same breadth, and after clamping iron strips to two opposite edges of the plates apply pressure perpendicularly to the surface of the plates. In this way one can compress the solids in one direction and cause them to elongate in another at right angles to the applied pressure. The appearance obtained is not unlike a surface view of the cambium of dicotyledons.

The plasticine is most easily recovered for use by shaking the solids from the experiment in a bottle of warm soapy water for a short time, rinsing with clean water, and then drying on a cloth in a warm place; most of the French chalk is removed so that the plasticine can be moulded into large masses.

A closer analogy to the conditions in a plant meristem would be obtained by using spheres of material that could be made to swell. Dry peas packed in a bottle and then soaked with water have been used, but with little success. A suggestion that pellets of dough be packed in a box and allowed to rise and then baked has been tried. The difficulty is to control the amount of swelling due to the yeast and early part of the subsequent baking.

SUMMARY

A method is described whereby spheres of plasticine may be pressed together and then taken apart so that changes in shape can be examined.

The effect of pressing spheres in various packings was tried. The most interesting case is that where closest packing gives solids resembling tetrakaidecahedra.

The writer is indebted to Professor J. H. Priestley for suggesting the problem and for his helpful criticism, and to the other members of the Botany Department for communicating their experiences with this problem.

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(1) PRIESTLEY, J. H. The meristematic tissues of the plant. *Biological Reviews,* **3,** 1. 1928.

(2) THOMSON, Sir W. On the division of space with minimum partitional area. *Phil. Mag.* (5), **24,** 503. 1887.

(3) TUPPER-CAREY, R. M. and PRIESTLEY, J. H. The cell wall in the radicle of *Vicia Faba* and the shape of meristematic cells. *New Phytol.* **23,** 136. 1924.

REVIEW

Plant Biology. An outline of the principles underlying plant activity and structure. By H. GODWIN, M.A., Ph.D. Cambridge University Press, 1930. Pp. ix + 265, with 67 figures in the text. Price 8s. 6d.

This book has been specially written to provide collateral reading to a course for first-year medical students in the University of Cambridge. It departs widely from the traditional text book of elementary botany, partly, though not wholly, on account of the reader to whom it is addressed, and the severe compression which has been necessary. It stresses the physiological and biochemical points of view, at the expense of the wealth of structural detail so beloved a decade ago. In this it is symptomatic of present-day tendencies, and as a reed to indicate the direction of the modern breeze it could hardly be bettered. If it leans a little heavily with the wind, that is of comparatively small account.

The impression left by a first reading of the text is one of surprise at the immense amount of information that has been packed within less than three hundred pages, intended as the printed companion to not much more than a dozen lectures. To get into these narrow limits an informative account of the life of plants and its "physico-chemical background," has naturally involved the omission of much that would ordinarily be expected under the heading of "Plant Biology," and opinions will inevitably differ as to the wisdom of the omissions. The most notable of the author's sacrifices are the reproduction of flowering plants, and any serious treatment of "alternation of generations" in lower groups. Cambia and secondary thickening, except in *Fucus,* are also passed over. The plant types selected for description have necessarily been few, but they are judiciously chosen and skilfully described to exhibit general principles such as the development of sex and soma, the differentiation of tissues and organs, and division of labour. It seems a little unfortunate, however, that speculative matter concerning phyletic origins has been allowed to enter into the description of so limited a range of types. Its influence upon elementary students is surely likely to be in the direction of loose rather than of exact thinking.

It is to be feared that the book will prove stiff reading to the average first-year student; and will, for the same reason, prove unsuitable for use in schools. A considerable knowledge of chemistry and physics is assumed, and when one finds the author describing (pp. 17 *et seq.*) the magnitude of colloidal particles, with hints concerning the methods of measuring them, one rather wonders what he would have advanced classes learn. It is probably impossible to explain

the chemistry of sugars without reference to stereoisomerism, but the matter having been raised, it certainly demands more than a footnote for its treatment.

The description of parenchyma on p. 191 becomes ambiguous because no comparison is made with meristems (previously described on p. 65), and it seems almost certain that an elementary student would gather that the two terms were synonymous.

On p. 22 appears the statement that "selective adsorption is very readily demonstrated by plants grown in water cultures, since in no case does the mineral composition of the adult plant correspond at all quantitatively with the mineral composition of the nutrient solution." It is true that phosphate, for example, is taken up by roots more readily than many other ions, but this is not necessarily due to a high affinity of phosphate for the adsorbing surfaces of the protoplasm. This ion is, in fact, readily converted into organic compounds, and so ceases to exist as phosphate inside the plant, although this does not appear from analyses of the ash. The uptake of other ions is presumably affected by similar considerations.

There are abundant line illustrations scattered throughout the volume, the great majority of which are models of their kind, and assist the text considerably. The book is well got up, is pleasant to handle, and on account of its matter well repays the rather severe task of mastering its contents.

W. O. JAMES.

ILLUSTRATIONS OF CARPEL POLYMORPHISM

VI

By EDITH R. SAUNDERS

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(With 24 figures and 4 diagrams in the text)

I T has already been shown that in the Rosaceae[1] we have an
illustration of the case where, on the one hand, genera with, as
a rule, numerous separate ovaries exhibit the condition in which *all*
the carpels are of the valve type, each forming an individual ovary
(*Potentilla, Rosa, Rubus, Dryas*). And, on the other hand, in contrast
with these few, a large number of genera in which a small carpel
number (10–2) is associated with polymorphism (most other rosa-
ceous types). A similar situation is met with in the Ranunculaceae
(compare e.g. *Anemone* and *Clematis* with *Nigella*)[2]. In the same
category with these two families we may include the Phytolaccaceae
which are dealt with in the present account. In this latter family,
however, as will appear, the retention of numerous carpels is not
invariably associated with monomorphism. For besides the section
including genera having typically ten (though sometimes as few as
five or as many as fifteen) monomorphic (valve) carpels, and another
in which all forms have fewer than five carpels and show poly-
morphism, there is a third group which exhibits polymorphism,
although the carpel number is sometimes far in excess of the
maximum found in the monomorphic section. The Phytolaccaceae
have a further special interest from the present viewpoint owing to
the fact that the few-carpelled polymorphic class includes forms which
have hitherto been regarded as having a single terminal carpel, but
these, like other cases of this kind (Berberidaceae[3], some Rosaceae[4],

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[1] "Carpel Polymorphism II," *Ann. Bot.* **41**, p. 570, 1927.
[2] *Report, British Association for the Advancement of Science*, p. 389, 1929.
[3] "Illustrations of Carpel Polymorphism II," *New Phytol.* **27**, p. 175, 1928.
[4] *Loc. cit.*

most Leguminosae[1], Sparganiaceae and Typhaceae[2], Pandanaceae[3], most Gramineae[4]) have proved on investigation to be, in reality, bicarpellary.

<div align="center">PHYTOLACCACEAE</div>

<div align="center">1. *Phytolacceae* (Figs. 1–5, Diagram A)</div>

Flowers ☿, ovaries generally several, becoming more or less completely free from one another. *Carpels as many as ovaries, in one whorl, monomorphic.*

In the species examined, viz. *Phytolacca clavigera* W. W. Smith (Figs. 1–4), *P. acinosa* Roxb. (Fig. 5), *P. decandra* L., *P. dioica* L., *Ercilla spicata* Moq., the number of ovaries varied between ten and five. Transverse sections show the residual vascular tissue serving the gynoecium as a continuous ring in which are to be seen from five to ten xylem strands. These strands, with accompanying phloem, furnish the midribs of the several carpels. As the carpels are all of valve form and become partly disjoined, the number of the xylem strands corresponds to the number of ovaries as well as to the number of carpels present. When the full complement of strands develop

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[1] "Illustrations of Carpel Polymorphism IV," *New Phytol.* 28, p. 225, 1929; also *Ann. Bot.* 39, p. 142, 1925.
[2] "Carpel Polymorphism III," *Ann. Bot.* 43, p. 459, 1929.
[3] Account not yet published.
[4] "Carpel Polymorphism I," *Ann. Bot.* 39, p. 155, 1925, and *New Phytol.* 27, p. 59, Fig. 55, 1928.

Figs. 1–5. Phytolacceae. All from transverse sections at successively higher levels. 1–4. *Phytolacca clavigera* W. W. Smith. 1. Gynoecium base from a flower with ten carpels in the whorl. The residual vascular ring shows ten xylem bundles. The main portion of each of these bundles turns out later towards the periphery to furnish the corresponding carpel midrib. In the centre is a large area of parenchyma (pith). 2. The same. Each of the ten bundles seen in the preceding section has given off a single placental strand; this strand and the corresponding midrib stand on the same radius. 3. The gynoecium at the level at which the ten midribs (seen cut longitudinally) turn out to the periphery. In the pith are small groups of discarded, undifferentiated vascular elements. 4. The same after the appearance of the loculi. The carpel midribs have given off further lateral veins. The pith has come to an end, giving place to a central space, and the carpels are already beginning to separate from each other at their inner face. Each carpel shows a small patch of conducting cells around the indentation where its margins meet. 5. *P. acinosa* Roxb. The gynoecium base partly surrounded by the disc, from a flower with only seven carpels to the whorl. Two carpel midribs after giving off the placental strand have turned out to the periphery, branching again as they go. The midribs of the other five carpels have not yet turned out from the centre.

ct, conducting tissue; *d*, disc; *dvt*, discarded vascular tissue; *s*, space.
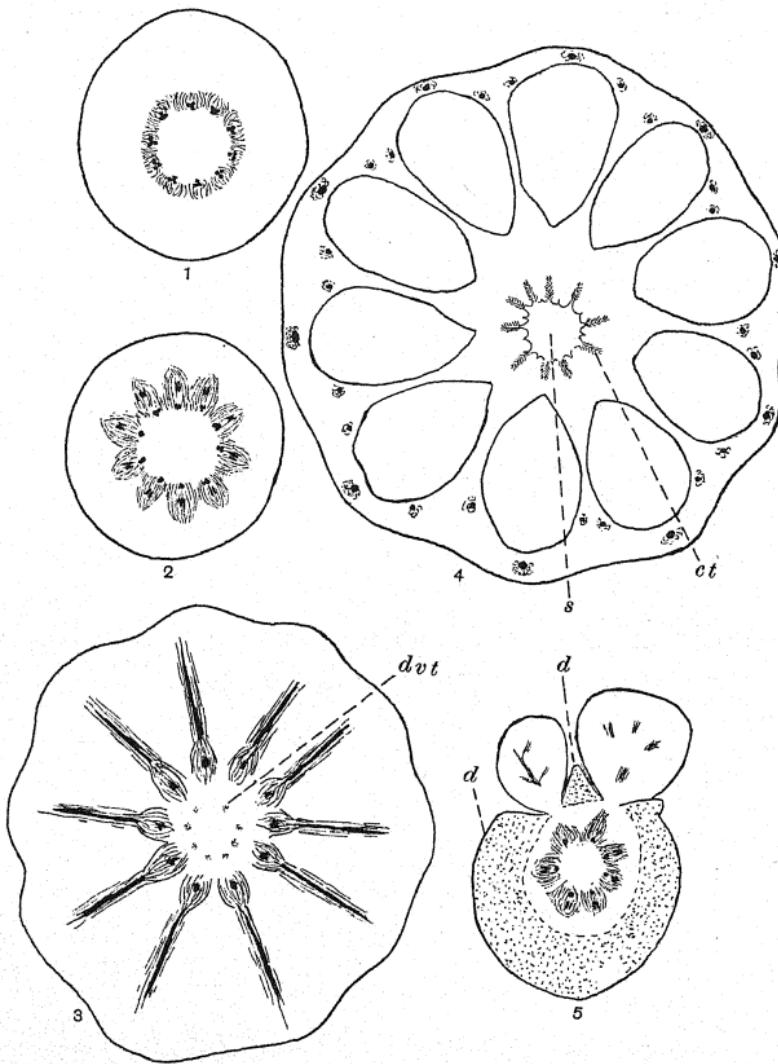
they stand at equidistant points on the circle, but in the case where some fail to differentiate those that die out may lie on adjacent radii, or again, on radii alternating regularly or irregularly with those on which xylem appears. It follows that sometimes an individual ovary may, at its origin, be separated by a considerable interval from its neighbour on one or both sides, and hence may at first develop more vigorously than its fellows until re-adjustment takes place. This asymmetrical condition was particularly marked in the case of *Ercilla spicata*, in which only five carpels are usually present; but in *Phytolacca dioica* with the same carpel number the surviving xylem units were regularly disposed on five alternate radii. Carpel development in this latter type is evidently a function of position (ante-*v*. alternisepalous), whereas in *Ercilla* this is clearly not the case.

The ovaries (= carpels) are united for a short distance at the base, laterally with each other and centrally with the pith, but are disjoined above, and as the pith comes to an end become entirely free.

In both genera a single median placental strand is given off below the level of the loculus by each out-turning carpel midrib, and this fertile strand is wholly used up in supplying the ovule, so that above the level of attachment of the funicles there remain only the carpel midribs and the later formed, right and left, lateral veins which constitute the secondary venation system of the valves.

As has been previously stated, the case of *Nandina domestica* (Berberidaceae) furnishes the only example so far met with in these investigations of the condition hitherto supposed to be of universal occurrence in the polymerous ovary, viz. that of complete union of the component, ovule-bearing, supposedly valve-carpels, only two in number in this particular instance[1]. Falling as far short of complete syncarpy as the merely basal union of the 5–10 carpels of the Phytolaccceae does, it appears, nevertheless, to represent the nearest actual approach to the conventional conception, the said dimerous *Nandina* alone excepted. *Platystemon* (Papaveraceae), formerly held to show partial union of fertile valve carpels, we now know must be otherwise interpreted[2]. Where, however, carpels showing some lateral expansion are *infertile*, complete syncarpy in a whole whorl will, presumably, present less mechanical difficulty, and does, in fact, occur in the outer whorl forming the ovary wall in Primulaceae[3].

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[1] See "Illustrations of Carpel Polymorphism II," *New Phyt.* **27**, p. 175, 1928.
[2] See "Illustrations of Carpel Polymorphism V," *New Phyt.* **29**, p. 47, 1930.
[3] See "Carpel Polymorphism I," *Ann. Bot.* **39**, p. 154 and Fig. 66, 1925.

2. *Gyrostemoneae* (Figs. 6–12, Diagrams C, D)

Flowers unisexual, ovaries in the ♀ flower disposed round a persistent central column of parenchyma (pith), to which they remain attached after becoming free from one another. *Carpels in two whorls, polymorphic, and twice as many as the number of ovaries.*

The amount and arrangement of the residual vascular tissue differ from that characterising the Phytolacceae, and give proof of the presence of a second carpel whorl.

Codonocarpus cotinifolia F. Muell. (Figs. 6–9). In this species the ovaries are described as ranging from twenty-five to fifty, disposed in one whorl. Hitherto they have been looked upon as composed of a single carpel, but a study of the vascular anatomy makes it evident that two carpel whorls are present—the number in the specimen figured being thirty-six in each, those of the outer whorl being of valve form and fertile, those on the alternate radii solid and sterile.

In a cross-section through the flower base the midrib bundles for the outer valve carpels are seen cut longitudinally as they turn out from the centre towards the periphery, their exit from the centre being followed by the appearance of the loculi. The residual stele then appears as a broad continuous ring in which xylem strands singly, or in groups of two or three, occupy positions neither quite in line with the loculi, nor midway between them where a patch of mechanical tissue indicates the junction line of adjacent carpels (*r* in Fig. 6). These single strands, or groups of strands, are composite units which shortly become resolved into the following parts: (*a*) a single placental strand in line with each loculus, (*b*) two bundles lying nearer the centre, one on each side of this strand, with or without (*c*) a remnant of varying size bordering the pith (Fig. 7). There is thus to be seen at this level in successive rings, from without inwards, the midribs of the outer carpel whorl which generally give rise to one or two pairs of sterile lateral veins; the placental strands of these carpels; a ring of bundles which later converge in pairs on the radii alternating with the loculi, these pairs eventually consolidating into the midrib cords of the second carpel whorl (Fig. 9); a final inmost ring of bundles that will be discarded (Fig. 7). It will be evident from this description that the gynoecium in *Codonocarpus* has a more complex structure than in the Phytolacceae, in which the residual vascular tissue only suffices for the midribs and placental strands of one carpel whorl. But the simpler constitution of the Phytolacceae points the way to the understanding of the forms con-

structed on a more complex plant. Without such indication, they might well have presented some difficulty. With this clue the interpretation seems clear. The outer whorl of valve carpels in *Codonocarpus* is comparable with the single carpel whorl of the Phytolacceae.
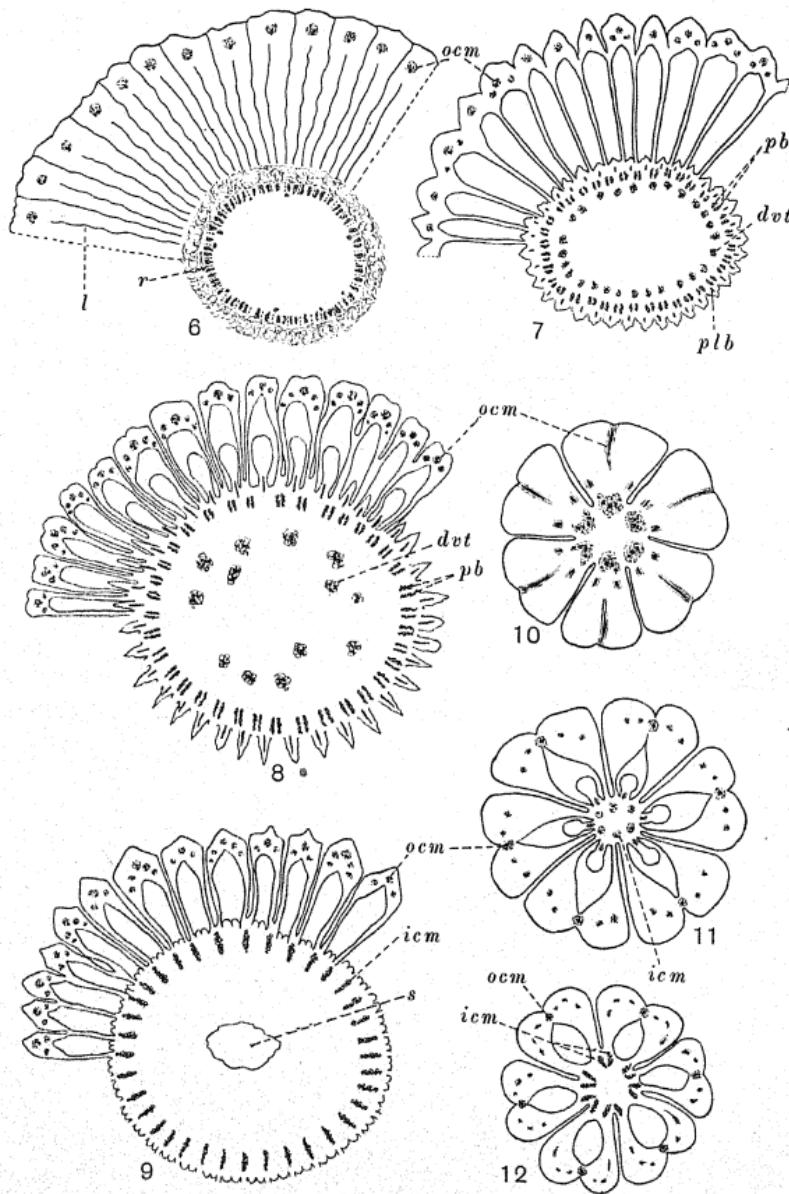
Figs. 6–12. Gyrostemoneae. All from transverse sections taken at successively higher levels. 6–9. *Codonocarpus cotinifolia* F. Muell. From a specimen with thirty-six carpels in each whorl. 6. The axis with some of the outer thirty-six carpels. Towards the periphery of the arc of the gynoecium the midribs of the sterile carpels in line with the developing loculi (indicated by slightly sinuous radial lines). In the centre a complete vascular ring with thirty-six single or composite groups of xylem elements lying in the sectors between the radii (shown by short interrupted lines) coinciding with the lines of contact between adjacent carpels of the outer whorl. Here and there on the inner face of the ring are additional strands, containing xylem as well as phloem, which will eventually be discarded. 7. The same after the appearance of the loculi. The midribs of many of the outer carpels have given rise to peripheral lateral veins. In the centre the placental strand of these carpels is now disjoined from the vascular elements associated with it in the preceding figure. Some of these latter elements now constitute a ring of twin bundles which later become consolidated into the thirty-six cords of a second carpel whorl. Within this ring is a further ring of bundles which enter the pith and are discarded. 8. The same at the level of origin of some of the ovules. The placental strands are turning out bodily into the ovules. In the centre, several discarded bundle masses of xylem and phloem. 9. The same above the ovule level. The placental strands have all passed out into the funicles. Hence the central ring now shows only the thirty-six cords of the second carpel whorl, whereas in the preceding figures the central vascular scheme, apart from discarded elements, involved a ground plan of seventy-two radii. The carpels of the outer whorl are becoming disjoined from one another. The discarded vascular elements have come to an end, and the pith, which will shortly disappear altogether, has given place to a cavity in the centre. 10–12. *Gyrostemon australasicus* Moq. From a specimen with six carpels in each whorl. 10. Gynoecium base. Towards the periphery, the midrib bundles (seen cut longitudinally) of the outer, solid carpels. In the centre, and on the same radii, a corresponding number of bundle masses not yet fully resolved into their components, but from which branches have been given off which are extending outwards in the radial walls. 11. The gynoecium at the level of attachment of the ovules. The placental strands of the outer carpels are now detached from the vascular elements associated with them in the preceding figure. These latter elements have become consolidated into the cords of a second, semi-solid whorl, standing on the alternate radii. From these cords arise the veins seen in the lateral walls of each ovary. 12. The same above the ovule level. The placental strands having passed out bodily into the funicles are no longer seen. The ovaries are beginning to separate laterally from each other, a process which involves the radial splitting in half of the members of the inner carpel whorl and the break-up of their main cords into their twin component bundles.

    dvt, discarded vascular tissue; *icm*, inner carpel midrib; *l*, the loculus appearing as a mere slit; *pb*, pair of bundles which later consolidate to form the inner carpel midrib; *plb*, placental bundle; *ocm*, outer carpel midrib; *r*, radius coinciding with the line of junction of two of the outer carpels; *s*, space.

In both cases the midribs, as they turn out from the centre, leave behind a single placental strand (which eventually passes bodily into the funicle) and later branch again to furnish the secondary veins of the ovary walls. This whorl, the only one present in the Phytolaccaceae, is followed in the Gyrostemoneae by a second whorl of consolidated, sterile carpels whose midrib cords of twin bundles, differentiated at a slightly higher level from the composite units mentioned above (shown in Fig. 6), alternate with those of the outer whorl. From this second carpel whorl there is left over in *Codonocarpus* yet another ring of bundles. These latter bundles are not utilised, but coalesce into irregular masses here and there in the pith (Fig. 8), and finally end blindly. It is to the presence of this large amount of residual vascular tissue supplying the second carpel whorl and furnishing an unusual quantity of discarded xylem elements that the belated appearance of the placental strands of the outer whorl is due[1]. At the level at which these placental strands and the vascular elements of the alternating inner carpels become distinct, the number of radii on which the vascular units making up the central ring are distributed are twice as many (here seventy-two) as the number of loculi (Fig. 8), but after the placental strands have passed bodily into the funicles the number of radii occupied by upward continuing bundles equals the number of loculi (here thirty-six), with which they alternate (Fig. 9).

Gyrostemon australasicus Moq. (Figs. 10–12). In *Gyrostemon* the number of ovaries is much fewer (5–8), being six in the specimen here figured. The plan of construction differs in some respects from that of *Codonocarpus*. The elements left behind in the centre after the exit of the outer carpel midribs are not in groups of separate strands but are consolidated into large unit masses lying on the same radii as the outer carpel midribs. From these unit masses branches extend outwards, even below the level of the loculi, into the side walls of the ovaries (Fig. 10), whereas in *Codonocarpus* the secondary veins are derived from the fertile carpel midribs. Development from this point onwards follows the same course as in this latter genus. The middle portion of each unit mass becomes differentiated into a placental strand in line with the midrib from which it arose when the latter turned outwards. The lateral portions diverge. This course brings together the two adjacent portions of

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[1] Belated, that is, in assuming a recognisable individuality by becoming dissociated from the remaining residual vascular elements, *not* as regards the time at which they branch off from the midrib bundles.

neighbouring masses, which fuse and so give rise on the alternate radii to the midrib cords of the inner (here semi-solid) carpel whorl which is sterile (Fig. 11). At the level of origin of the ovules the placental strands turn out bodily into the funicles as in the preceding types (Fig. 11). Above the ovule level separation of the ovaries is brought about by a median splitting of the semi-solid carpels from without inwards (Fig. 12). At the same time the midrib bundles of these carpels become resolved into their two component bundles, so that as the split extends to the pith each ovary comes to consist of a whole solid carpel and the half of the semi-solid carpel on each side, i.e. of $\frac{1}{2}$ 1 $\frac{1}{2}$ carpels, a construction with which we are now familiar in many other instances.

The two genera, *Codonocarpus* and *Gyrostemon*, are thus alike in that both have two carpel whorls, the outer being the one which is fertile. They differ in that in *Codonocarpus* the outer carpels are of the valve type, the inner are solid, and a considerable quantity of vascular tissue is discarded, while in *Gyrostemon* the outer carpels are solid, the inner semi-solid and but little vascular tissue is discarded.

3. *Rivineae* (Figs. 13–24, Diagram B)

Flowers almost always ⚥. Ovary solitary, *usually composed of two carpels, one valve and sterile, the other solid and fertile,* hitherto considered to be formed of a single terminal carpel.

In each of the three genera investigated (*Rivina, Ledenbergia, Petiveria*) the valve carpel forms the wall of the ovary and bears either a sub-terminal style (*Ledenbergia, Rivina*) or one very distinctly lateral[1], with a brush-like stigma (*Petiveria*).

Ledenbergia rosea-aenea Lem. (Figs. 13–15). At the flower base the residual vascular tissue for the gynoecium appears as a ring of several bundles, all but two consisting solely of phloem or undifferentiated elements, the two which develop xylem lying opposite one another in the median plane. At a little above this level all the residual phloem becomes aggregated round the two xylem bundles, which become the midribs of one fertile and one sterile carpel, respectively (Fig. 13). The lateral branches of the sterile midrib extend round the whole circumference of the ovary wall, in which can clearly be seen the line of junction of the meeting edges of the valve above the level of origin of the ovule, i.e. the level at which the fertile carpel comes to an end (Fig. 14). The whole construction

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[1] I.e. not terminal. As regards *radial* position both style and stigma arise in the median plane.
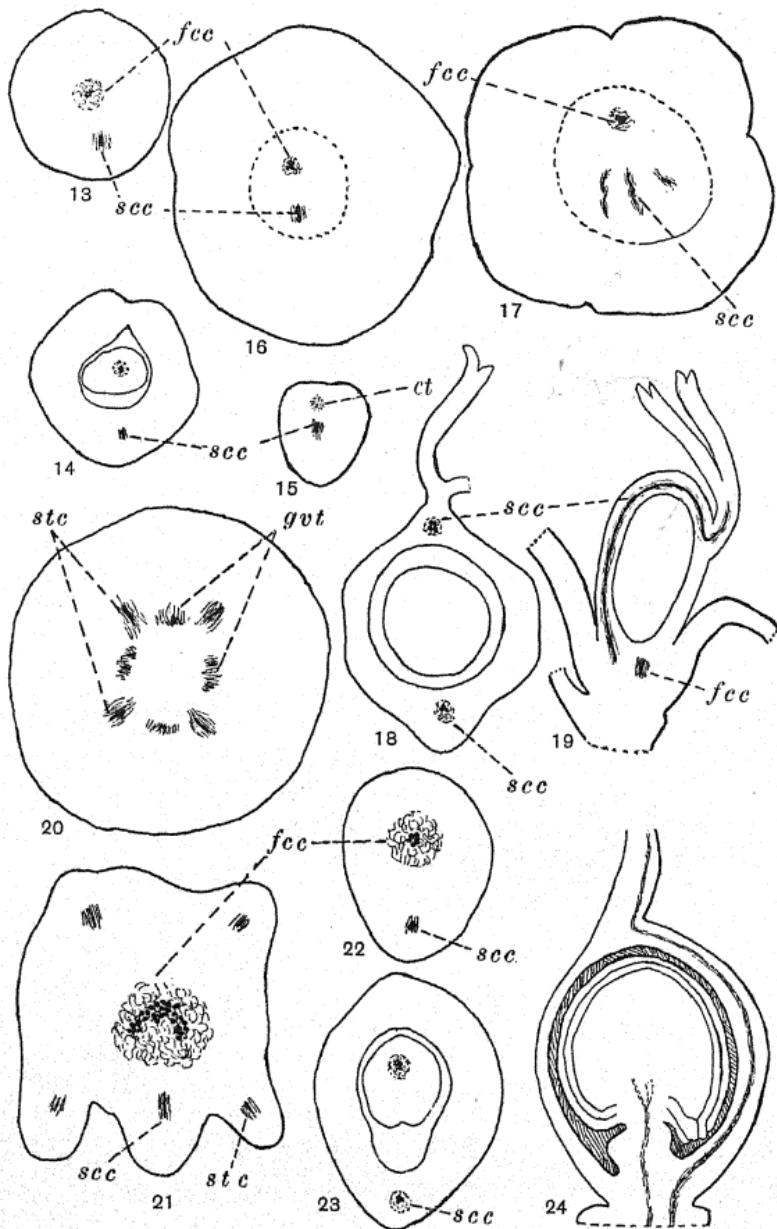
of the gynoecium is thus similar to that of certain other types hitherto regarded as monocarpellary, as e.g. *Pandanus* and *Sparganium*. As the loculus closes it gives place to a core of conducting cells (Fig. 15) which come to the surface on the ventral side at the top, where they pass into the cells of the brush-like stigma.

Petiveria alliacea L. (Figs. 16–19). A cross-section taken below the level at which the outline of the ovary area becomes defined shows the whole of the centre region occupied by, as yet, undifferentiated vascular elements, the pith being completely obliterated. Within this area and at opposite points arise two groups of xylem (Fig. 16). One of these bundles turns out horizontally to furnish the midrib and secondary veins of the sterile carpel; the other continues upwards to become the unbranched cord of the fertile member

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Figs. 13–24. Rivineae. All from transverse sections at successively higher levels except 19 and 24. 13–15. *Ledenbergia rosea-aenea* Lem. 13. Gynoecium base below the level of the loculus, showing the vascular cords of the two carpels. 14. The gynoecium after formation of the loculus. At this level the ovary wall is formed wholly of the sterile (valve) carpel, the fertile (solid) member having come to an end at the level at which the ovule arises. 15. The same after the loculus has closed. Towards the ventral face a patch of conducting cells. 16–19. *Petiveria alliacea* L. 16, 17. Flower base. The boundary of the gynoecium is defined, but the tissue is not yet disjoined from the perianth. The cord of the fertile carpel is cut transversely, that of the sterile carpel, which has begun to turn outwards in 16, and in 17 has given rise to lateral veins, is seen cut longitudinally. 18. The gynoecium after the fertile carpel has come to an end. (Only portions of two filaments of the much branched feathery stigma are represented in this and the following figure.) The sterile carpel midrib is seen cut twice, in its upward course (below), and after it has curved round over the top of the ovary (above). The unequal development, in other words the difference in length between the front and back carpels, causes the short style to arise about halfway up the ovary side. 19. The same in longitudinal section, showing the whole course of the sterile carpel cord. Below the loculus, the cord of the fertile carpel. To right and left, the cut ends of the perianth members. 20–24. *Rivina humilis* L. 20. Flower base. The vascular bundles for the four stamens are about to turn out from the central ring in the diagonal planes; on the alternate radii the residual bundle masses for the gynoecium. (For the sake of simplicity the vascular bundles of the perianth have been omitted.) 21. The same after the perianth members have been exserted. At the corners the bundles for the four stamens; towards the front the bundle destined for the sterile carpel; in the centre the massive cord for the fertile carpel. The boundary of the ovary is not yet defined. 22. Gynoecium base below the level of the loculus showing the cords of the two carpels. 23. The gynoecium after development of the loculus. The wall of the ovary is formed by the sterile carpel, the fertile carpel having come to an end at the level of origin of the ovule. 24. The gynoecium in longitudinal section showing the two separate vascular cords of the two carpels. (24 after Walter, *Pflanzenreich*, **83**, p. 103, Fig. 30 F.)

ct, conducting tissue; *fcc*, fertile carpel cord; *gvt*, vascular tissue for the gynoecium; *scc*, sterile carpel cord; *stc*, stamen cord.

(Fig. 17). The stigma in this genus forms a brush of filaments borne on a style shank which takes origin part way down the ovary wall (Figs. 18, 19). This lateral position is caused by the bending over of the apex of the sterile carpel, as is shown by the course of the midrib bundle which curves round the top of the ovary, and continues down the opposite side until it again turns upward to enter the style base (Fig. 19)[1]. Consequently cross-sections of the ovary taken from any level between the origin of ovule and style have a midrib bundle on the one side only, but sections taken above this level show a bundle on both sides, since at these levels the sterile carpel midrib will be cut twice (Fig. 18). As in *Ledenbergia*, the meeting edges of the valve can be plainly recognised after the termination of the fertile carpel at the level of origin of the ovule.

Rivina humilis L. (Figs. 20–24). Transverse sections taken through the base of the flower after emergence of the perianth cords show four equidistant vascular bundles in the diagonal planes, which pass out to the four stamens, and somewhat nearer the centre on the alternate radii four bundle masses bordering the pith (Fig. 20). At a slightly higher level the anterior bundle of these four passes out from the ring (Fig. 21) and becomes the midrib of a valve carpel giving off lateral veins on its way. The other three xylem groups no doubt in an ancestral form supplied three other carpels, but in the present-day type they converge and become consolidated into a large semicircular mass (Fig. 21) which continues its upward course (Fig. 22), furnishing the bundle to the ovule (Figs. 23, 24). Above the level of origin of the ovule the ovary wall shows the sterile carpel midrib with a few lateral veins derived from it, which however extend only part way round the circumference. The manner in which the residual vascular elements are utilised in the construction of the gynoecium has some features in common with *Alchemilla*, one of the most reduced types among the Rosaceae. In *Alchemilla*, which also has a tetramerous ground plan, the residual vascular tissue available for the gynoecium consists of four bundles on radii alternating with those of one whorl of perianth segments, and coinciding with those of the other[2], a distribution suggesting that in some ancestral form four ovaries were present. In the Peruvian *A. nivalis* H.B. and K., indeed, three still survive[3], though in most living species there is

only one. In the species with a solitary ovary so far examined, none of these four strands retains its individuality. All four converge and become consolidated into a single cord—the midrib cord of the solid, fertile carpel. If the sac portion of the ovary is correctly interpreted as formed from a second, sterile, valve carpel, then this second carpel has lost its vascular elements. In *Rivina* the four residual masses likewise lie on the radii alternating with those of the preceding whorl[1]. Here, however, one of the four remains distinct and supplies the sterile member. The other three become consolidated into a single bundle—the cord of the fertile member. The fact that the valve carpel bundle persists as a well-developed strand in *Rivina* is probably correlated with the fact that here this carpel is the one which produces the style, whereas the sterile member in *Alchemilla* performs no function beyond that of protecting the ovule.

Figures showing the appearance in the earliest stages of development of the gynoecium of *Rivina* and *Petiveria* are given by Payer in his *Organogénie*. From his drawings it is obvious that the view that only one carpel is present will not cover the facts if the ovule is held to be borne by the carpel itself. This was evidently appreciated by Payer, who adopted what then appeared to be the only alternative solution, viz. that the ovule arises from the axis. The conception of carpel polymorphism, as formulated above, fully accounts for the position of the ovule and removes the necessity for postulating any anomalous relation in respect either of the carpel or the ovule.

SUMMARY

1. The three sections Phytolacceae, Gyrostemoneae and Rivineae of the family Phytolaccaceae differ in regard to the constitution of the gynoecium.

2. In the Phytolacceae the carpels, varying in number from five to fifteen, stand in one whorl and are all of the valve type as supposed hitherto.

3. In the Gyrostemoneae the carpels, whether few or many, contrary to received opinion, are in two whorls; the outer whorl being fertile, the inner sterile. In *Codonocarpus cotinifolia*, with from twenty-five to fifty in a whorl, the outer whorl is of the valve type and the inner is solid. In *Gyrostemon australasicus*, with from five to eight in a whorl, the outer carpels are solid and the inner semi-solid.

[1] In this case the staminal whorl, in *Alchemilla* the inner perianth whorl since the stamen cords pass out conjoined with those of the outer perianth members.

Floral Diagrams
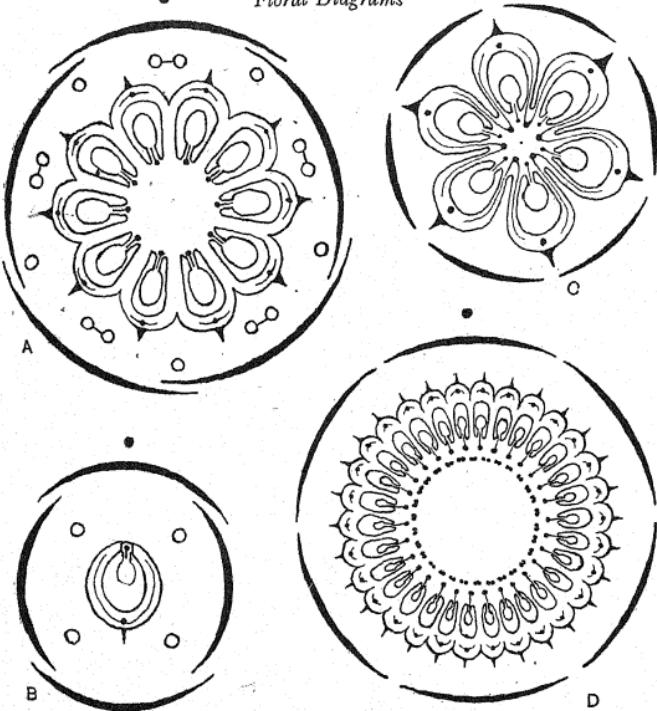
A. *Phytolacca decandra*. G 10, monomorphic, in one whorl, valve, fertile,
syncarpous below, becoming apocarpous above. Style filaments terminal,
in line with the loculi, each of one carpel.

B. *Rivina humilis*. G 2, polymorphic, one anterior, valve, sterile with style;
one posterior, solid, fertile, without style.

C. *Gyrostemon australasicus*. G two-whorled, polymorphic. The carpels of the
outer whorl solid and sterile, those of the inner whorl semi-solid and fertile.
Style filaments each of $\frac{1}{2}$ 1 $\frac{1}{2}$ carpels, in line with the loculi. [From a
specimen with hexamerous whorls.]

D. *Codonocarpus cotinifolia*. G two-whorled, polymorphic. The carpels of the
outer whorl valve and fertile, those of the inner whorl solid and sterile.
Style filaments each of $\frac{1}{2}$ 1 $\frac{1}{2}$ carpels, in line with the loculi. [From a
specimen with 30 carpels in each whorl.]

4. In the Rivineae the ovary, hitherto regarded as constructed of a single terminal carpel, is shown to be bicarpellary (*Ledenbergia, Petiveria, Rivina*), one carpel being of the valve type and sterile but bearing the style (if present) and stigma, the other being solid and fertile.

The list of families in which the anomaly of the solitary terminal carpel has now been found to have no reality includes, in addition to the Phytolaccaceae, the Berberidaceae, Rosaceae, Leguminosae, Typhaceae, Sparganiaceae, Pandanaceae and Gramineae.

The conclusions formulated above are exhibited in the floral diagrams on p. 94.

STUDIES IN THE PHYSIOLOGY OF CAMBIAL ACTIVITY

II. THE CONCEPT OF SLIDING GROWTH

By J. H. PRIESTLEY

(With Plate II and 17 figures in the text)

CONTENTS

INTRODUCTION

THE essential thesis in the present series of papers is that the fusiform cambium initials, as growth units, are potentially equivalent to the meristem cells of the shoot or root apex in the same plant, but are growing under a different internal environment. They are, as a result, very different in shape and size, and it is very difficult to visualise how the almost iso-diametric cells of the growing point could be transformed into the radially compressed, elongated meristem cells of the cambium ring. Still more difficult is it to realise how these elongated cells, after transverse division, can change in position so that they come to lie side by side with one another in the cambium ring. Usually the difficulty is met by the statement that these changes in relative position are brought about by "sliding" or "gliding" growth (*gleitende Wachstum*). This concept

is by no means so simple as it may appear at first sight. It was first introduced by Krabbe((15), English readers will find a very full review in the *Annals of Botany*(29)), and has never been very seriously examined since, though difficulties in the way of its acceptance have occasionally been raised (10, 20, 21, 25, 33). Sliding growth in a complex living tissue has naturally not been observed in progress; it is inferred from the successive stages in cell arrangement as revealed upon microscopic examination. It is the intention of the present paper to point out that the assumption is unnecessary in many cases where its occurrence has been assumed, on these grounds, as the result of Krabbe's classic paper, and that certain lines of indirect evidence suggest that it is not justified. In fact, this concept of sliding growth has never been really critically examined because, when the successive relative positions of the cells are agreed upon, it has seemed to most investigators that a sliding growth is the only process by which these adjustments in cell position could take place. Before, therefore, a critical examination will carry weight with most readers, it is necessary to show that an alternative method exists, by which these changes in cell position could be brought about, and which does not involve sliding growth.

Considerable space is given, therefore, in the following pages to the explanation of an alternative method in which these changes in cell position may take place. This alternative is as much a hypothesis as the theory of sliding growth, but it seems to be in better agreement with the nature of the cells which are thus undergoing change of shape and position and with the structure of the walls and the alignment of the cells in the adult tissues which have resulted from the activity of the cambium. It would seem essential to put forward this alternative method of growth and argue the case for it fully because, until such an alternative method of growth is before the mind of the reader, he will accept the idea of sliding growth, whatever the difficulties, *faute de mieux*.

All the cases of sliding growth considered by Krabbe will not be re-examined, but only those which are relevant to our present problem of the growth of the cambium and its derivative tissues. It is suggested, however, as the result of this limited re-examination of the subject that *all* cases of sliding growth cited by Krabbe require critical re-examination.

The concept of sliding growth

The assumption involved in the concept of sliding growth is that two cells such as A and B of Text-fig. 1 may move relatively to one another, so that the wall of A slides over the surface of the wall of B. The relative position of the two cells is thus altered and the regions of the wall of A and B which previously corresponded with one another, WX to YZ in Text-fig. 1, no longer correspond, but parts of the wall surfaces now either face upon intercellular space or are in contact with the wall of a different cell. Under certain conditions, which are of limited duration in the growth of the plant(23), such movement would certainly seem possible. Thus if both cells are turgid to the point of rigidity, and if the middle lamella between the two cells is of a plastic, yielding nature, then, given the necessary
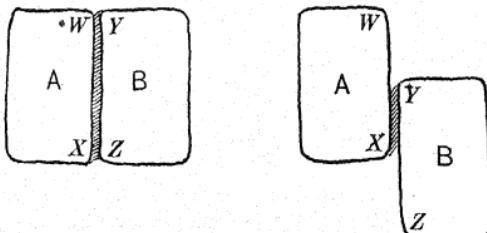
Text-fig. 1. Alteration of cell position by "sliding growth."

shearing force, A may slip over the surface of B. If, however, the middle lamella is set to a hard, dry cement, this movement will not be possible and it is very unlikely to take place if A and B are not turgid with stretched, elastic walls. Thus A and B may be meristem cells, with plastic, inelastic walls, so that the cells are not rounded at the corners and there are no intercellular spaces. As both these plastic cellulose walls and the intervening middle lamella are interpenetrated by numerous protoplasmic connections, it is very difficult to visualise how any shearing force can be developed in the tissue which will carry A past B. On the other hand, if A alone is turgid with stretched elastic wall, and B is still meristematic, then whilst A is thus expanding under the osmotic forces developing in the vacuole within, some slight shift of the wall of A in reference to the wall of B seems very possible, though not necessarily inevitable.

The difficulty of producing a considerable movement of cell A past B, as a whole, when both cells are plastic, meristematic units,

has been felt by many writers, and sometimes the attempt is made to get over the difficulty by assuming that whilst A and B may not move past one another as a whole, local growth of these cells, usually restricted to the ends, may modify their mutual positions. This point of view is better considered when a specific case of its utilisation is before us. It will then be found that all the difficulties which arise when a close examination is made of the concept of sliding growth in its simple form, are still present when there is substituted for it this concept of a local sliding growth.

It seems impossible, on *a priori* grounds, to decide whether the relative movement of cells involved in sliding growth is practicable or not under the conditions existing in developing tissues. Fortunately a very valuable criterion seems to exist which may decide whether such relative movement has occurred in adjacent walls. Practically all developing walls are interpenetrated by protoplasmic connections or plasmodesma (16, 18). Strasburger has disposed very completely of the tentative hypothesis that these plasmodesma were the remains of the spindle threads seen in the later stages of cell division in suitably fixed material (33). In this case they would only be found in certain walls. Actually they are normally found in every wall in the young cell, except any wall which may find itself on the outer surface of the plant. When protoplasts separate from one another upon division, the new boundary wall between them is never a continuous surface. From the beginning it is penetrated by the protoplasm at different points. As this new wall surface grows in the meristem cell, the cellulose surface increases in area, and these protoplasmic breaks in the cellulose also increase in size. But, apparently, as they do so, cellulose deposition takes place *within* the enlarged area derived from the original plasmodesmon so that, instead of a continuous protoplasmic area in the wall, a *group* of protoplasmic connections between adjacent protoplasts is found. Secondary cellulose deposition, when it occurs later in the vacuolating cell, takes place where the surface of the protoplast lies against the continuous cellulose areas of the primary wall, but not immediately around the plasmodesma or groups of plasmodesma, which are thus left as pits in the wall. When, therefore, no displacement of the original neighbouring walls has taken place, these pits face one another across the middle lamella and are said to correspond. Whilst the protoplasm fills the cells, these pits are places where the plasmodesma are seen to penetrate the wall. But if, during development, one wall moves relatively to the other, a very slight movement will shear all these

protoplasmic connections. If this happens very early, the plasmodesma will probably withdraw from the wall, cellulose deposits will now be laid down all over it and no pit will be found. The plasmodesma threads may not withdraw from the walls after their rupture, possibly because pit formation has already commenced; in this case the pits will still be formed but will no longer correspond in position across the middle lamella. Both cases may be met with and both provide strong indirect evidence of the occurrence of slip during development.

It is frequently assumed that protoplasmic connections may reform after their first destruction (Strasburger(33), Sharp(30) chap. III, p. 67), but there is no direct evidence in support of this assumption; in fact, Strasburger points out that he has never seen plasmodesma connections re-established after their rupture by plasmolysis. This re-establishment of plasmodesma connections requires that the protoplasm should penetrate the continuous cellulose surface lining it. Mechanical penetration of the cellulose gel by the colloidal protoplasm seems very improbable, and there seems to be no reason why, at one spot, the protoplasm should be digesting the cellulose at the same time that it is depositing cellulose over the rest of its surface. No case whatever, therefore, seems to have been made out so far for the production of such secondary protoplasmic connections.

The evidence for sliding growth will be examined, therefore, on the presumption that the presence of plasmodesma and corresponding pits is evidence that no slip has occurred between the walls on which they appear, whilst the absence of pits or their failure to correspond will be regarded as indirect evidence that slip has occurred during development.

The alternative to sliding growth

When cells are seen in different positions relative to one another, at different stages during development, it is argued that such changes in relative position *must* arise by sliding growth. This argument will prevail unless it can be shown that such a change of position *may* be brought about in another manner. An alternative method for the changes in cell position in the apical meristem was briefly indicated in a previous paper(23). As this alternative method will apply also to the more difficult case of the cambium, it must now be described more fully, and it is desirable to explain in the first place how the changes in cell shape, and adjustments in the rela-

tive position of cells, may thus be brought about in the apical meristem.

Adjustments of cell shape and cell position in the apical meristem

Consideration of a series of microtome sections of any apical meristem will convince any observer that such changes in cell size, cell shape and cell position must continually be taking place. Thus, for instance, every new division wall first meets the old wall at right angles but, except in the outermost cell layer, such cell walls are subsequently seen to meet each other at angles approximating 120°. It is difficult to think one's way through the changes in cell shape and position therein involved, in the solid, and it will probably
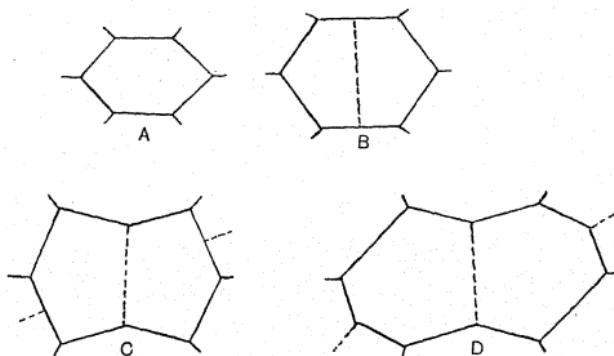
Text-fig. 2. A–D. Progressive changes in cell shape during the course of cell division in the meristem. New walls are dotted.

prove simpler to follow first of all the changes in cell shape as they would be seen in a series of optical sections of the process. These changes are diagrammatically illustrated in Text-fig. 2, A–D. These figures illustrate a twelve-sided meristem cell, in continuous contact on all twelve surfaces with other meristem cells, as seen in optical section throughout the process of cell division and subsequent readjustment of shape. In section, each point of the hexagon is a point where the cell is in contact with, at least, two neighbours. As the growth of all these cells is about equal and the tension in their walls is approximately the same, an equilibrium position is attained when the walls meet at this point at an angle of 120°; to this position they are always tending.

But as the result of cell division a new wall appears in this cell, which first meets the old walls at right angles. How will this new point, where three cells are now in contact, attain an equilibrium position? Like all their neighbours these two new cells are growing, and as they increase in size they gradually adjust their relative position so that the shape alters from that shown in Text-fig. 2 B to that in Text-fig. 2 C. They will still appear pentagonal, but the new walls are now meeting the older walls in a position which is nearer equilibrium in view of the tensions in the walls. This new position can be reached, however, without any slip between the wall of the cell and its neighbours; each threefold common wall, composed of cellulose layer, middle lamella and cellulose layer, grows and stretches as a common "three-ply" membrane, without the necessity of any slip between the two cellulose surfaces. The return of these new pentagons to the original hexagonal symmetry will probably wait upon new cell divisions in neighbouring cells. The way in which these may bring about this change is illustrated in Text-figs. 2 C and D, where the new walls in the neighbouring cells are shown as dotted lines.

Considering this plane projection of an optical section of one out of the mass of semi-fluid protoplasts with plastic walls growing under tension, it is possible to visualise these changes in cell shape in an individual cell as it grows in size after its formation in cell division and until, in its turn, it itself divides. In a section of any plane the same type of change would be seen, and all cells are behaving similarly. The fundamental conclusion is that the adjustments of cell shape and cell position are taking place as a result of a gradual, *mutual* adjustment of position in which the partition walls adjust their tension and position as *a common framework*, without the necessity for any slip between any two cellulose walls facing one another across a common middle lamella. That adjustments do take place in this manner, without sliding growth, is certainly suggested by the existence of plasmodesma, and subsequently of corresponding pits, in all walls in the parenchyma that differentiate from this apical meristem. Between procambial strand and parenchyma, that is, between meristem cell and vacuolated cell, slip may occur under some conditions. But the study of the cell adjustments in the procambium raises similar problems to that raised by the study of the cambium, where there are more data available for discussion.

GROWTH AND CELL DIVISION IN THE CAMBIUM OF THE
ELONGATING SHOOT

As was pointed out previously, the cambial cells are in continuous connection through meristematic cells with the meristematic cells of the shoot apex. In fact, they are cells of exactly the same type, engaged in the same work, but under different conditions. An outstanding difference is that cambial cells are under much greater pressure in a radial direction, owing to the vacuolation and extension of the cells of the pith and cortex. The result is that the cambial cells are flattened. When so flattened they might be expected to spread out either tangentially or longitudinally.

Tangentially there is resistance to such movement, because the cells form a continuous cylinder; vertically, on the other hand, they naturally extend because in this direction the movement is facilitated by the rapid vertical extension of the files of vacuolating parenchyma in pith and cortex, which are similarly extending as the result of repeated transverse division. Thus, as the internode elongates, the cells of cortex and pith at first multiply rapidly in number and extend in length slowly; then for a time they elongate rapidly, as they vacuolate and cease to divide. The procambial elements which remain meristematic extend in length under compression and divide transversely, but at relatively infrequent intervals.

These long cambial elements are considerably shorter in radial dimensions than the apical meristem cells, but they are so much elongated that their mass is much greater than the isodiametric apical cell; at the same time, of course, the necessary ratio of surface to mass is maintained in an element of this type. Being compressed units which originally were more or less twelve-sided, they should still appear hexagons in all three planes of section (Text-fig. 3), and so they have been found in the Dicotyledons by Beijer[4] and Kleinmann[11]; in the Gymnosperms, where the radial pressure is much greater, there is only an occasional suggestion of this original shape in the appearance of the cells in the tangential longitudinal section.

As the vascular tissue differentiates from the tissues formed from the cambium after repeated tangential division of these elongated initials, the vacuolation and expansion of the xylem elements within increases the pressure upon the elongating elements and under these circumstances they elongate still more. The first-formed vascular elements are pulled out and elongated by the continued elongation of the parenchyma in which they are embedded. In this

manner then, so long as the elongation of the shoot continues, the cambium ring keeps pace with it and the cessation of shoot elongation leaves us with a ring of elongated cambium initials. During this elongation stage it would seem probable, from Kleinmann's and Beijer's observations, that most, if not all, the cell divisions by which cells are multiplied in the cambial ring take place by transverse walls, both in shoot and root. In Dicotyledons, with "stratified" cambia, as soon as growth in length ceases, the multiplication of cells in the cambium ring takes place by longitudinal radial divisions.
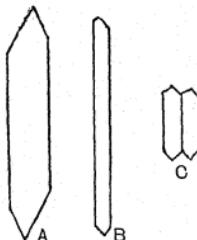
Text-fig. 3. A–C. Cambium cells (typical of Dicotyledon with stratified cambium) as seen in (A) tangential longitudinal, (B) radial longitudinal, and (C) transverse section. (After Beijer and Kleinmann.)

Text-fig. 4. Position of new wall (dotted) on its first appearance during radial longitudinal division of a cambium cell. (After Beijer.)
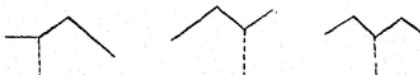
Text-fig. 5. Appearance of these walls (of Fig. 4) after adjustment of cell position (as seen in tangential longitudinal section).

The cause of this type of division is not investigated at this stage, but Beijer's observations make it abundantly clear that, following each cell division in this type of cambium, the readjustment of these plastic, meristematic cells continues exactly in the manner discussed for the apical growing point. Thus, in radial longitudinal division Beijer points out that the new wall never runs to the pointed apex, but adopts one of the forms shown in Text-fig. 4, and that following such division, observed, of course, in tangential longitudinal section, the series of cells gradually readopts the original type of grouping (Text-fig. 5).

This change is watched, of course, by following its record as left in the successive layers of elements cut off from it, and can be followed in the changes of form of the cell as a whole in Text-fig. 6. Similarly, in transverse section, Beijer records the change from A to B in Text-fig. 7. Kleinmann's figures show exactly similar cell adjustments.

With reference to the old controversy as to the existence of one or more cambium initials, it would now seem desirable to regard the whole depth of the ring in which, as seen in transverse section, this type of cell adjustment was taking place, as meristematic and there-

Text-fig. 6.

A   B
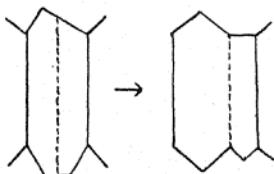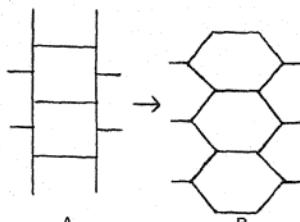
Text-fig. 7.

Text-fig. 6. Changes in cell form, following longitudinal radial division in the cambium, as seen in tangential longitudinal section. (After Beijer.)

Text-fig. 7. A, B. Cambium cells as seen in transverse section, following tangential divisions, alter from the arrangement shown in A to that shown in B, without any sliding growth. (Figures after Beijer.)

fore cambium. This ring would vary in breadth at different seasons and, furthermore, its relative position might alter a little farther inwards or outwards (Nordhausen(21)), but it would always be recognised by the same essential characteristics of cell growth and division.

Beijer regards these changes in cell form and position as taking place by "sliding growth," but they are clearly exactly the type of changes we have been following in the apical meristem. They are now taking place in elongated cells, but they can be produced in the same manner without any relative movement of the cell walls on either side of the same middle lamella.

GROWTH AND CELL DIVISION IN THE CAMBIUM OF THE CONIFER AFTER THE FIRST YEAR

When a shoot of the tree ceases growth at the end of the first year, longitudinal extension in that portion of the shoot is complete. Radial growth may continue year after year in this segment of the

axis, but there will be no change in the longitudinal dimensions of
this segment of the cambium, save for relatively unimportant
changes connected with branching that may be neglected at this
stage (see p. 134).

Under these conditions the soft-wood and the hard-wood tree
each presents its own special problem of interpretation. In the
Conifer the great puzzle is provided by the fusiform initials which
may continue to grow in length in the cambium in a segment of the
trunk in which longitudinal extension as a whole has finished.
Bailey has shown that this increase in length continues for many
years and, furthermore, that when a fusiform initial divides to
increase the number in the meristematic cylinder, it divides trans-
versely and then the new cells once more grow to at least the original
length (2, 3).

In the hard-wood tree, where the fusiform initials may increase
very little in length, an equally puzzling problem is provided by the
development of the fibres, which may grow to several times the
length of the fusiform initials from which they are derived, long
after growth in length of the portion of the axis in which they are
formed has ceased. The soft-wood and hard-wood trees, therefore,
provide us with two very different problems which require entirely
separate consideration.

In the present section the growth of the Conifer cambium will be
considered. Bailey has supplied very valuable data for this case,
such as the figures for *Pinus strobus*, which were utilised in the first
paper (24).

The growth of this meristematic cylinder, the Conifer cambium,
raises some extraordinarily complex problems which are very
inadequately dealt with when the case is dismissed with the state-
ment that the elongating fusiform initials grow in amongst one
another by sliding growth. An adequate description of the growth
of this layer would be very difficult to give. The best way to approach
the problem seems to be to assemble the facts so far as they are
available, with some examination of the sources of information, and
then to pass in review the difficulties in the way of their interpreta-
tion on the hypothesis of sliding growth. We shall then be in a
position to reconsider these facts and their interpretation from the
alternative standpoint as to the manner of meristematic growth
developed in the previous section.

The data

The main facts as to the growth of the cambium cannot be better presented than by reconsidering the data for *Pinus strobus* already supplied. In sixty years the periphery of the cambium has increased one-hundredfold. The numerical data supplied by Bailey and previously cited have been converted into diagrammatic form in Text-figs. 8 A and B. A strip of cambium of equal longitudinal

A   B
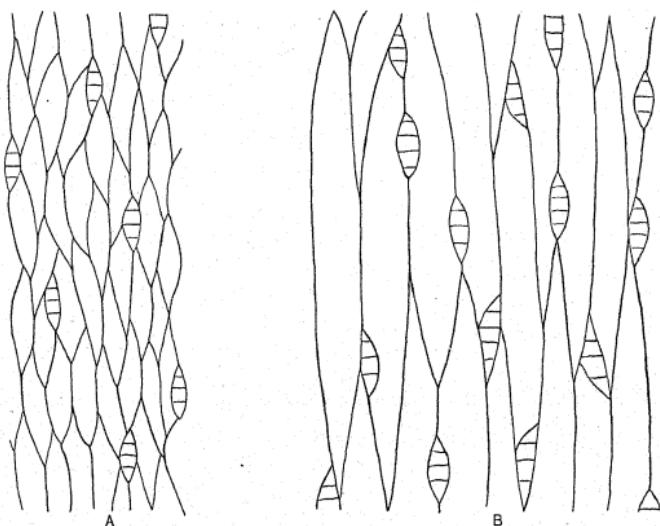
Text-fig. 8.

    A. Diagrammatic representation of a strip of cambium of *Pinus strobus* as seen in tangential longitudinal section in a one-year-old shoot.

    B. Part of the same strip of cambium 60 years later. It has now increased to 100 times the original width but the vertical height is unaltered. The changes in cell size and in number of ray initials are roughly to scale but, for practical convenience, the vertical scale is 1/100 the horizontal scale. (From data supplied by Bailey.)

dimensions is represented in these diagrams and upon it is shown, in Text-fig. 8 A, the distribution of fusiform initials and ray cells in this strip of cambium at the end of the first year. In Text-fig. 8 B, the cells are drawn to the same relative scale, and they show the alteration in the relative size and number of fusiform initials and ray cells in such a strip of cambium by the end of the sixtieth year. Whilst these diagrams are roughly to scale, in order to make them of

practicable dimensions it has been necessary to make the vertical
scale one hundred times smaller than the horizontal scale. Actually
the fusiform initials, in tangential section, when they look as wide as
this, would appear one hundred times this length (see photos 1 and 2,
Plate II).

The fusiform initials have grown much larger but they are
proportionately still longer than before. The ray cells at any level
have increased from about one in ten of the cells in the ring to
between one in two, or one in three, but at the same time their
actual dimensions have altered but little.

Fewer cells can be shown in Text-fig. 8 B, but if it is remembered
that the width of the whole strip would be one hundred times that
of the whole strip of cambium shown in Text-fig. 8 A, it will be seen
that actually the total number of fusiform initials present must be
much greater. The numbers have already been given; including ray
cells, the number of cells in the periphery in a section have increased
from an approximate 800 to about 32,000.

The increase in the area and the change in form involved when
Text-figs. 8 A and B are contemplated, and when it is realised that
the strip, Text-fig. 8 B, should be 100 times the width of Text-fig.
8 A, seem so remarkable that it is very necessary to emphasise that
the change in size and form has been very slow and gradual as the
cylinder of cambium is carried out upon the expanding surface of
the wood. It was pointed out (23) that, in the course of these sixty
years in any genetically connected series of fusiform initials, only
between three to five transverse divisions have taken place.

We have next to consider how these changes in cell size and cell
position have taken place. It is advisable first to consider how we
may hope to gain information on this point. Unfortunately no
method is available enabling one to watch the living cambium layer
as it grows. We must, therefore, reconstruct the process. This may
be done either by examining sections of the cambium layer, cut at
different times and different ages, or by trying to reconstruct the
changes that have taken place by tracing the change in shape and
position in the cells derived from the cambium layer. It seems to the
writer that the first of these methods is much the more reliable but,
since the publication of a paper by Klinken (12), the second method has
been much in favour, so that the point deserves closer examination.

Throughout its whole life the cambium initial is repeatedly
cutting off replicas of itself, to the inside and to the outside, through
the successive tangential longitudinal divisions by which elements

are added either to xylem or phloem. With relatively little distortion in the Conifer, these elements subsequently become part of the permanent tissue. If, therefore, a series of tangential longitudinal sections are cut, it should apparently be possible to trace the changes in outline of the fusiform initials in the course of time by the changes in form of the elements derived from them. Klinken applied this method, cutting tangential longitudinal sections of the phloem of *Taxus baccata*, on the assumption that the phloem was less distorted during differentiation.

The phloem is certainly more easily cut—it is doubtful if it is less distorted. The differentiating phloem elements do not change appreciably in length, but as they are thrust farther to the outside by the expanding wood they are frequently displaced tangentially, so that the radial lines of elements in the phloem, as seen in transverse section, have often a very wavy outline. This is not only true of sections taken from the tree; if an objective is used in which the light is sent through the lens and reflected back into the microscope, it is easily possible to see that the radial rows of phloem are similarly distorted at the cut end of the stem before the section is made.

By trimming a block of phloem asymmetrically it is, however, possible for the observer to orientate himself in such a series of tangential longitudinal sections, so as to identify the same rays in successive tangential sections and, therefore, to look at the form of the elongated phloem elements between the rays. The same methods have been adopted by subsequent workers and Beijer's figures of changes of cell form, utilised in the previous section, were obtained in this manner. A method, however, which may be trusted when used, as by Beijer, to trace changes of form in cells which are little longer than broad, may not serve for cells of the shapes derived from these extraordinarily elongated fusiform initials, which (as we may again emphasise) are relatively one hundred times as long as they are shown in Text-figs. 8 A and B. The phloem of *Taxus baccata* was re-examined from this point of view. Klinken's sections, he states, were 30 μ thick. From a piece of phloem 3 mm. thick from a forty-year-old stem he cut 100 sections; he rejected the ten outer sections and based his case for the changes in form of the cambium initials upon the remaining ninety sections.

When the radial diameter of the phloem elements is examined, the sieve tubes at their widest are just about 30 μ in diameter, near the cambium they are much less than this; farther out they tend to be rather flattened tangentially. Clearly no vertical section can hope

to follow continuously, throughout its length, the same sieve tube or
chain of phloem parenchyma. Consequently a vertical wall figured
in Klinken's diagrams may be the radial wall corresponding to the
original radial walls of the fusiform initial from which such a phloem
element was derived, but, on the other hand, it is equally likely to be
the edge of a tangential wall where the knife is passing from one
vertical element to another in a different tangential plane.

From this standpoint it is very doubtful whether the representa-
tion of changes in cell form provided by Klinken's diagrams give a
better picture of the actual changes in form undergone by the
growing cambium initial than can be gradually reconstructed by
direct observation of the various forms of cambial cell seen in
examination of tangential sections through the cambium. It is in
this way that all our reliable data have been obtained. Thus Bailey
has seen and figured the nuclear division in the transverse division of
the initial (3). That all divisions are of this type is abundantly clear
from the general appearance of the cambium in tangential longitu-
dinal section (Phot. 1, Plate II). If the cells occasionally divided by
radial longitudinal division, an occasional sign of a "stratified"
cambium, with the apices of the two neighbouring cells at the same
horizon, would necessarily be seen. Other points also are at once
apparent: for example, the rays are so numerous that practically
every fusiform initial is in contact with at least one ray in some
portion of its course, and many are in contact with more than one
(Janse (9)). Another point of interest is that every point of a fusiform
initial meets the walls of two neighbours: in no case is a point simply
invaginating another tracheid, so that no initial is forked and there-
fore forked tracheids are unlikely to occur (see p. 129).

Confronted with the problem of interpreting these extraordinary
structures, since Krabbe's paper botanists have usually dismissed
them as developing by "sliding growth." Bailey has pointed out
that some such process seems to be necessary to take the points of
two daughter cells, derived from one fusiform initial, past one
another—they certainly must move because the cambium cylinder as
a whole is undergoing no elongation. Similarly, during its elongation
from a length of 0·8 mm. to 4 mm. in *Pinus strobus*, the fusiform
initial will be thought of as thrusting its extending length in between
the neighbouring initials.

Difficulties presented by sliding growth in the Conifer cambium

All the slip between these various initials as they slide past one another must take place along the radial walls. This mode of growth then should be associated with subsequent lack of plasmodesma and pits upon the radial walls. But the facts do not correspond: in the xylem, plasmodesma have been found in the young radial walls (Hill(6)); later, corresponding bordered pits are found in abundance on these walls, whilst plasmodesma (Hill(6)) and pits are missing from the tangential walls, except that pits sometimes appear on the outside of the annual ring in the tangential walls of the last few elements of the summer wood. Similarly in the phloem, the sieve tubes have numerous sieve areas on the radial walls but none on the tangential walls.

The suggestion is sometimes made that this difficulty may be overcome by assuming localised regions of growth in these initials. It is clear, however, that an apex sliding between two neighbouring cells must separate the plasmodesma originally connecting these neighbours, and that when an initial grows from 0·8 mm. to 4 mm. a considerable amount of sliding movement is involved, in fact, it is very doubtful whether, when sliding is assumed, any portion of the radial wall can be assumed to be stationary. Such an hypothesis also involves the assumption that in a meristematic cell certain parts are growing, others not—a new complication. It also suggests that in the derivative tissues some parts of the radial wall should be structurally different from others—no trace of such a difference can be found, apart of course from the uniformly distributed pitted and non-pitted areas.

In other words, localised growth of the apices or certain regions of the initials in no way removes the difficulties in the way of this type of interpretation and receives no support from observations on the tissues derived from the cambium. But there are certain other facts about the secondary tissues and especially the wood of the Conifer which have to be harmonised with any interpretation of its mode of growth, and with these we must now deal.

Sanio's "rims" and Sanio's "trabeculae"

Sanio first described a structural feature of the radial wall of the tracheid which has been very fully discussed of recent years as Sanio's "bar" or "rim." Sifton(31) gives a very full account of the literature. The structure is only of interest to us at the moment, in

that it appears on the radial wall at a very early stage of differentia-
tion [28] which makes it clear that its position is determined in the
growth of the fusiform initial and that like the pits, with which it is
associated, the position of this "rim" always corresponds in the two
walls which face one another across a middle lamella. In other words,
Sanio's "rim" is good evidence against any slip between the two
radial walls. On the other hand, if the position of these rims or of the
pits is compared in a series of neighbouring tracheids in a radial
longitudinal section—a comparison that must be made with care as
the section may easily glance off into another radial row of tracheids,
so that the radial walls are not equivalent—there *is* evidence of a
gradual shift of vertical position in rims and pits in *radially successive*
tracheids. As they are presumably formed from the same original
groups of plasmodesma in the radial wall of the fusiform initial,
which will be replicated in every successive element cut off from it by
tangential longitudinal division, these vertically shifting pits and
Sanio's rims are evidence that, in time, the radial walls of the fusi-
form initial are moving vertically, but without any slip between the
two walls facing each other across a middle lamella.

The trabeculae, which Sanio first noticed in a Dicotyledon [26]
but subsequently reported from the pine [28], are a more difficult
problem still for the exponents of sliding growth, who seem with
great unanimity to have ignored them. But though only occasional
in their occurrence, they are universally present in Coniferous
secondary tissues. A history of the subject will be found in Müller's
paper [19]. His investigations and those of Raatz [25] show that they
are present in all types of Conifer, in the secondary tissues of root,
trunk and twig, and that, whilst they may only occasionally be seen
in a transverse section, the careful exploration of any secondary
tissues, especially in longitudinal tangential section, will very soon
reveal their presence.

These trabeculae are thin plates or bars of cellulose (they have
sometimes also been called "bars of Sanio" [7] so that, to avoid
confusion the term "bar" is not used in this account either for rims
or trabeculae) which cross the lumen of the cell from one tangential
wall to the other; they are never found running tangentially from one
radial wall to the other. Occasionally these trabeculae have apparently
been formed in the young tracheid as it differentiates, in this case
they occur singly; in other cases they have appeared in a fusiform
initial, or at least in a cell which is still dividing tangentially, if only
for a short time. In the last case the trabeculae are found running

through a short series of cells; but if they occur in the fusiform
initial itself, and thus finally in all the derived cells dividing tangen-
tially in the region of the cambium, then they occur in long radial
series, running through both xylem, cambium and phloem. Such
trabeculae may persist through many annual rings, and it is this
type which is so important in the present connexion, because,
examined in transverse section, the trabeculae run straight out
without any tangential displacement: examined in radial longitudinal
section they run continuously outward without any indication of
vertical displacement, either up or down, in successive elements of
the radial series. If, then, the fusiform initial traversed by such a
"balk" or trabecula of cellulose is moving vertically and sliding over
its neighbours, it is also moving relatively to this rod of cellulose,
much as a plank may move past the bandsaw cutting it: only, in
this case, the two sides of the initial, which have moved down either
side of the trabecula, join up again immediately they are past the
trabecula and show no sign of its point of passage. Each trabecula is
connected not only with the cellulose lamella, but the pectin of the
middle lamella of the tangential walls can often be seen to be in
connection with a central pectin staining region of the trabecula
which has a different refractive index from that of the surrounding
cellulose.

It is clear that before sliding growth can be accepted as an
adequate account of the movement of these fusiform initials other
possibilities of cell adjustment should be thoroughly explored. There
are very real difficulties in reconciling such sliding on the radial
walls, with the position of the pits and protoplasmic connections in
the derivative tissues, with the corresponding Sanio's rims facing one
another on either side of the middle lamella of the radial walls and
with the radial path of the trabeculae through the lumen of xylem
element, cambium initial and phloem element.

The re-interpretation of cambial growth given in the next section
may be regarded as a first contribution to such an explanation.

A re-interpretation of the growth of the cambium cylinder in the Conifer

It will never be possible to understand this extraordinary process
until our direct observation of sections under the microscope is
completed by a mental reconstruction of the nature of this cylinder
of cells and the conditions under which it is growing. Undoubtedly
the protoplast of each fusiform initial is of fluid consistency, very

probably showing protoplasmic streaming during life, and these liquid contents are enclosed in a plastic, inelastic wall which will deform under tension. The whole cylinder is pressed outwards on the surface of the differentiating wood so that the tangential longitudinal walls will be under considerable tension, whilst the liquid contents are pressing equally, of course, on both radial and tangential walls. There are no transverse walls in this system and when such a wall appears it is apparently in unstable equilibrium, presumably being itself rapidly drawn into a vertical position by the tension on the longitudinal walls to which it is attached. The fusiform initials thus form a very fluid system, deforming under pressure and readily adapting themselves to the change of position as they are carried outwards by the expanding wood. Scattered amongst them, everywhere, however are turgid, vacuolated, ray cells which are not so free to move. Each ray cell is expanded against its firm cellulose envelope, and therefore resists deformation. It has a much greater radial dimension than the fusiform initials, and presses firmly within and without upon the older cells of the ray. These, in their turn, are held rigidly against the surface of the fully differentiated elements in wood and phloem, with thick and often lignified walls, so that the rays represent fixed points amongst these semi-fluid fusiform initials.

As the cylinder expands and its surface grows greater, the fusiform initials grow commensurately, *i.e.* their size and the mass of their protoplasm increases and thus they continue to cover the wider area; on the other hand, the ray initials fail to do this. The vacuolated cells of the young ray grow and divide by tangential division so that their extension keeps pace with the increase in radial dimension of the woody cylinder, but they *do not increase appreciably in tangential surface area*. This point is of very great importance. An attempt is made to illustrate it diagrammatically in Text-fig. 9. Whilst the fusiform initial A_1 grows with the expansion of the ring (to A_2), B_2 in the older ring has the same tangential and longitudinal extension as B_1 in the younger ring. The result is that on the flanks of every ray, as the ring grows wider, a space would develop in the cambium cylinder if it were not that the fluid nature of the fusiform protoplasts enables them to cover this space so that all the time they remain in close contact with the ray.

As the cylinder of cambium is thus carried out, therefore, there must be, all the time, a slow shifting of the position of the stretched tangential walls. It will be very gradual and mainly the result of the

continued growth of the protoplasts, but the occasional transverse division of these protoplasts and the subsequent readjustment in relative position of the two daughter protoplasts involve a shift in position quite apart from growth.

This shifting in position will accompany the continual movement of these protoplasts into the spaces in the widening cylinder which would otherwise be uncovered on the flanks of the ever more numerous rays; it does not necessarily involve *slip*, because the change in
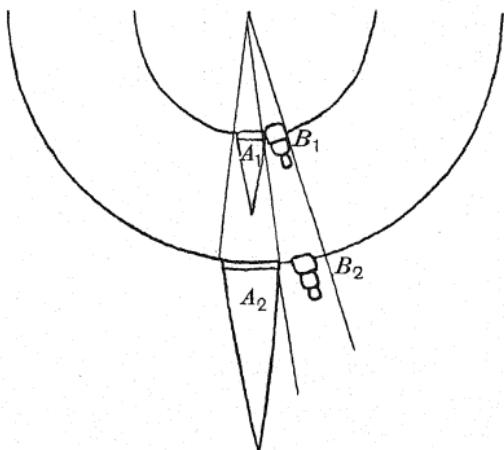
Text-fig. 9. Diagrammatic contrast of the tangential growth of fusiform initial and ray cell. As the ring of cambium expands, the additional periphery is filled by the growth of the fusiform initial but the ray initial fails to keep pace with this increase in periphery. As a result the fusiform initials will flow into the space shown as vacant on the flanks of the ray initial in the wider ring.

position occurs in a series of steps, in the newly formed tangential walls that are continually being laid down.

It is difficult to visualise the form changes in the individual initial which will accompany their gradual lateral expansion into the spaces on the sides of the rays. We know that these changes are associated with a continual increase in size of each initial, and that these changes in shape and size are associated mainly with increase in vertical length of the individual initial; we have also noted the fact that the occasional divisions in the growing initials are transverse and that the new walls relatively rapidly become nearly vertical, because tangential longitudinal sections of the cambium rarely show

walls which are at all transverse in direction. The whole process of change of form and position of the initial must involve mainly the shifting of these transverse and longitudinal radial walls, each wall moving as a "three-ply" system—wall, middle lamella and wall—without any slip between the individual initials. An attempt is made to illustrate the manner in which such form changes would occur, following a transverse division, in Text-figs. 10 A, B and C,
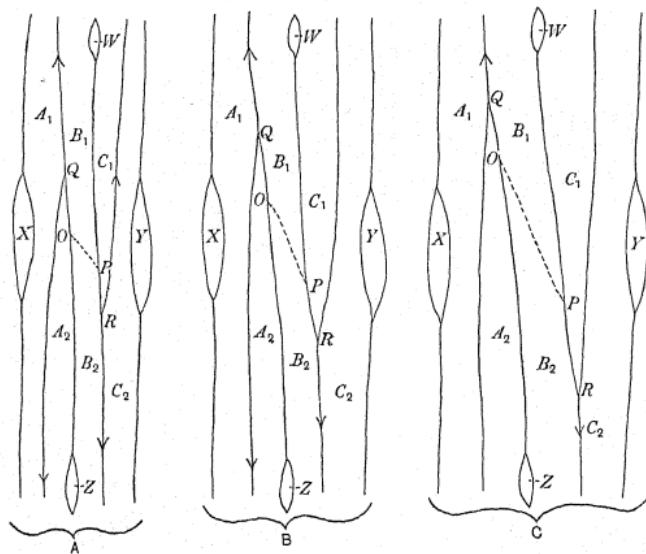
Text-fig. 10. A, B and C. A diagrammatic representation of the changes in cell position that follow a transverse division of the fusiform initial B into the two cells B_1 and B_2, as seen in tangential longitudinal section. For detailed discussion see text.

which represent the positions of a series of initials, lying between two rays X and Y, as seen in tangential longitudinal section, at successive intervals of time. During the period that elapses between Text-figs. 10 A and C, the two rays become farther apart in a transverse plane, as the cambium ring is pushed outwards, but the vertical distances between the rays, as between W and Z in these diagrams, do not alter if the cambium cylinder is vertical in this region. It is assumed that during this period only one transverse division takes place, that shown as a dotted line, separating B in the

cells B_1 and B_2; on either side the products of earlier divisions are shown as A_1 and A_2, C_1 and C_2; and these daughter initials continue to move past one another during this time. These various initials are shown as growing larger during this period, as they undoubtedly do, until a transverse division occurs and is followed by the gradual displacement of the contents of the two daughter initials, so that they come to lie partly side by side, when the widest part of the initial is replaced by two slender tapering cell extremities. Thus the widest portion of an original initial, B, is replaced during this period by the tapering ends of B_1 and B_2. It will be seen that the reorientation of the new division wall, OP, will occur as the longitudinal walls extend which separate B_1, B_2 from A_1, A_2 and C_1, C_2 respectively. In view of the position of the rays W and Z, the wall between $B_1 B_2$ and $A_1 A_2$ is shown as elongating upwards, that between $B_1 B_2$ and $C_1 C_2$ as moving downwards, since it is assumed that where the initial wall lies against the ray cells it will cease to elongate, or at least elongation must now be accompanied by slip, because on the side of the ray cell no equivalent vertical elongation is taking place. If slip has to take place, elongation will be accompanied by considerable friction, and may be expected to take place much more slowly. It is probably safe, therefore, in considering the general elongation of the fusiform initials, to treat the rays as fixed points and to regard the elongation of the wall as taking place in the region where the initials do not border on the rays. On this assumption, in the case figured in Text-fig. 10 A, the further elongation of the walls would certainly take the point O upwards and P downwards by the continued extension of the radial walls.

It is interesting to compare the different manner in which the tangential and radial longitudinal walls will have accommodated themselves to the change in position during the period of growth and division of a fusiform initial; the originally transverse division wall between B_1 and B_2 may be regarded for all practical purposes as an extreme case of movement in a radial wall in view of its final orientation, so that there are only tangential and radial walls to consider.

The new position is achieved by the tangential walls in a series of steps, because new tangential longitudinal walls were laid down in the cambium initial very frequently. During the period (of several years' duration) during which B grows and divides into B_1 and B_2, a number of tangential divisions will have taken place, each new wall being a little larger than the former one. Each wall when first laid down will be just such a wall as is usually formed across a dividing

meristematic cell, with plasmodesma penetrating it, and two cellulose lamellae facing one another across a thin middle lamella. Subsequently this wall will undergo considerable strain, tending to produce slip, because the inner tracheid initial will vacuolate and extend before the outer. The amount of slip thus produced may be small, but it is usually sufficient to rupture the plasmodesma. These were not found in this wall by Hill(6), and subsequently pits were not found in the tangential wall, save in the last elements of the wood formed, where the extension of the differentiating tracheids is least, and, as a consequence, the tendency to slip is also least.

On the radial walls in the cambium, on the other hand, the adjustment in size takes place as a continuous process of growth and extension of the same wall, of which fresh and larger slices are cut off between the successive tangential walls to contribute to each new xylem element formed; in these successive slices the number of groups of plasmodesma, i.e. of sites of future pits, will increase in the normal manner associated with the growth and extension of any meristematic wall. Again, of course, the wall is a "three-ply" structure, with two cellulose walls facing each other across a thin middle lamella. In this case, however, there is no tendency to slip, the cells on either side of the radial wall are of the same age, they are at first growing together and then, later, differentiating at the same time. The wall is originally penetrated by plasmodesma, and these, as Hill observed, form the sites of the future pits, so prominent on these radial walls.

When two new cells have come to lie side by side in the transverse section, as the lower pointed end of B_1 and upper pointed end of B_2 in Text-figs. 10 A–C, then a new radial series has appeared in the transverse section of the wood. This new series appears suddenly, in accordance with the new appearance of tangential walls in the dividing cells, but it is provided for by the gradual extension of the radial longitudinal walls of the parent cambium initial in the manner just described.

This conception of the cambium layer as consisting of semi-fluid fusiform protoplasts, lying between the fixed, vacuolated radiating groups of ray cells, fits very well with the subsequent distribution of the pits upon the walls of the wood and with the sieve areas in the phloem; it also agrees with the correspondence of the rims of Sanio on the radial walls, but can it be harmonised with the straight radial progress of the trabeculae of Sanio?

These trabeculae in the initials themselves are plastic masses of

cellulose, usually rather long, vertical lamellae joining one tangential wall of the initial to the other. The middle lamella in the middle of the trabecula suggests that the trabeculae arise as folds of the wall. Müller shows them sometimes, in tangential section, as a vertical series in the one cell, as if a fold of the radial wall had broken up into a number of isolated structures. Raatz regards them rather as formed by the union of the tangential walls of the compressed initial, the union not taking place right across the cell so that it does not form a transverse septum. Either view would seem possible, though the occurrence of rudimentary pits or even occasionally bordered pits on the flanks of the trabecula as seen in tangential section and described by Raatz, seems to point to their origin from the radial walls. These rather thick clots of plastic cellulose trapped between the closely adpressed tangential walls of the initial are transformed into the relatively thin and rod-like trabeculae when the differentiating cells undergo radial extension.

From the fact that the trabeculae, so long as they are present, travel straight out in an undeviating radial path in successive cells of a radial series, they represent fixed points like the rays and do not alter their position as we have seen that both the radial and tangential walls of the fusiform initials are doing. This is, however, quite intelligible. The tangential walls alter their position slowly and in successive steps, as a result of the growth of the protoplast, but the trabecula is fixed to a spot on the tangential surface of the initial which will not grow, because there is no protoplasm within the tangential wall at this point, and which will appear as a fixed point in each successive tangential wall. It is clear that the radial walls may alter their position without reference to the trabecula, to which they are not attached, and the fluid contents of the protoplasts will not bring any pressure upon the plastic trabecula to displace it. Ordinarily, as the fusiform initial grows larger, the radial walls, which may be very near the trabecula to start with—indeed the latter very probably begins as a fold of this radial wall—will usually get farther away from it, but it is possible that occasionally, as a transverse wall sweeps round to the vertical, a radial wall may come in contact with the plastic cellulose of the trabecula again. This may be a means of bringing about what Müller and Raatz speak of as the reabsorption of the trabecula, which may now again form part of the normal cellulose wall.

Fusiform initials and ray cells

During the growth of the cambium cylinder, some sliding move-
ment of plastic fusiform initial wall over the distended wall of the
turgid ray cell is possible and may account for the early obliteration
of plasmodesma between the ray cells and the young tracheids noted
by Hill, and also the failure of plasmodesma between starch-
containing ray cell and sieve tube (6). There need be no general
vertical movement of the radial walls of the fusiform initial bordering
the ray, however, and the wide common pit between parenchymatous
ray cell and tracheid suggests that these walls have for some time
extended in common without any slip, a process which, as Text-fig.
II shows, could readily occur, because the radial elongation of the
vacuolated ray cell keeps pace with the radial expansion of the young

                    A   B
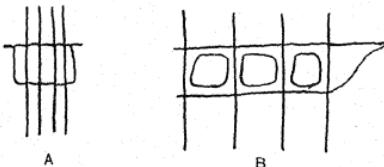
Text-fig. II. A, B. Radial expansion of ray cells and tracheids diagram-
matically illustrated in radial longitudinal section. The wall common to ray
cell and tracheid may expand radially without any slip, so that a wide common
pit results as shown in B.

tracheid. The wide common pit membrane and the narrow area of
thickened border in these cells, and in the tracheid where the ray
cell crosses it, suggests that most of this wall expansion has been
a stretching of a primary wall perforated with plasmodesma. Hill
has noted plasmodesma between a young tracheid and such a ray cell
in Pinus but regards it as probable that they are usually obliterated
during the later stages of development.

On the other hand the elongated ray cells at the top and bottom
of the narrow rays in Pinus (and also scattered at various heights
throughout the ray) have thickened walls and bordered pits, although
the pits do not usually correspond in position on the walls of tracheid
and ray that face one another. This suggests that at this point on the
ray there has been more slipping between the wall of xylem tracheid
and ray tracheid during development, and such slipping seems
particularly natural at the margins of the ray because, as is seen in
tangential section (Phot. 2, Plate II), the xylem tracheid wall meets

the ray tracheid wall in this case at a sharp slope. Indeed the question
may be raised whether the greater amount of slip thus produced,
together with an earlier rupture of plasmodesma and withdrawal of
the protoplast from the perforated area, does not account for the
utilisation of the living contents of these tracheids which line the
top and bottom edges of the ray in the deposition of secondary
lamellae, whilst in other ray cells protoplasm is retained and
occasionally employed in starch deposition, etc. A similar suggestion
can be applied to the retention of protoplasm, and the habit of
starch storage, in the outermost row or two of the wood elements at
the end of an annual ring in many Conifers.

Between the ray cells and the radial walls of the differentiated
phloem elements a different relationship exists in *Pinus.* It appears
that whilst the vacuolated central cells of the ray elongate in a radial
direction the cells lining the margin of the ray do not do so, but
remain densely packed with protoplasm. These cells apparently
stretch no more in a radial direction than the sieve tubes with
which they are in contact. The result is that the "albuminous" cells
on the top and bottom of the ray remain attached to the contents
of the sieve tubes by numerous plasmodesma, whilst no plasmodesma
are found between the sieve tubes and the starch-containing ray
cells (Strasburger(33), Hill(6)).

We have now passed in review the main structural features of the
secondary tissues derived from the Conifer cambium, and whilst we
have found many characteristic features of this tissue which seem
incompatible with the usual mode of growth assumed to take place
in the cambium, all of these features can be reconciled with another
method of visualising the growth process in the cambial layer—a
method which has been developed in the previous pages. This mode
of growth, slow mutual adjustments of cell positions, with changes
in cell size and shape, associated with a gradual adjustment of the
walls as a common framework, without slip between cell and cell,
may seem more difficult to visualise, but if the conception of sliding
growth is followed up till details of the process are grappled with,
this mode of growth will be found very hard to visualise also. This
new picture of the growth of these fusiform initials also harmonises
better with their true nature, with their fluid protoplasts and plastic
walls. Heilbrunn has recently summarised cogent reasons for
thinking that "in certain cells at least, the viscosity of the granule-
free protoplasm is only several times as great as that of water"(8)
and in the living protoplasts in the neighbourhood of the cambium,

in which Bailey has often seen vigorous streaming, we certainly have
relatively fluid protoplasts contained by thin, plastic walls.

VESSEL AND FIBRE DIFFERENTIATION IN THE DICOTYLEDONS

In the soft-wood tree, during its increase in girth, the outstanding
problem is the accommodation, in the same length of axis, of fusi-
form initials of increasing length. In most species of hard-wood tree,
after the first few years, the average length of the fusiform initial
changes very little, but a new problem presents itself: in an axis in
which longitudinal growth has ceased, fibres differentiate which are
many times longer than the cambium initials from which they have
been derived.

This is the first example of sliding growth dealt with by Krabbe
(15), and again further examination is necessary before this phrase is
admitted to cover the facts of development. In this case there is no
doubt that slip occurs between the wall of the expanding vessel and
the walls of the cells surrounding it. Thus, in *Quercus* or *Fraxinus* in
the uniform tissue first formed from the cambium, the future vessel
element, in transverse section, is seen in continuous contact with
some six cells of about the same size. After its expansion, the vessel
has torn apart some of these neighbouring cells, splitting the con-
nection between them along the middle lamella; it thus comes in
contact with additional cells, lying in more distant radial rows and,
less frequently, more distant tangential rows. The vessels of these
plants, as seen in transverse section, may thus finally be placed in
contact with as many as thirty cells, and naturally, where this type
of vessel expansion occurs, either no pits are present between the
vessel and some of the neighbouring elements, or the pits present
fail to correspond.

But at the same time, the expansion of the vessel has compressed
some of the neighbouring elements, with plastic walls and fluid
protoplasmic contents. These elements have, as a result, become
much elongated and, according to Krabbe, their pointed ends slide
between each other and over the surface of the vessel. It is this
type of sliding movement, particularly that taking place between
fibre and fibre, which must not be accepted without closer examina-
tion. Krabbe points out that the first indication of this movement,
as seen in transverse section, is the appearance of fine, narrow
angular cells between the regular radial rows of young wood elements.
These radial series continue to be displaced in this manner and by
the expansion of the vessels in irregular order until, except for the

unbroken radial path of the rays, all indications of the regular radial order in the wood may disappear.

Before the development of the elongated fibres around the expanding vessel segments is attributed to sliding growth, there are various difficulties to be considered.

In the first place, if the fibres become three times as long as the cells of the cambium from which they are formed and if they slide amongst one another in this manner, they should become three times as numerous in cross-section during differentiation. Reference to Bailey's data [2] will show that the average length of the fibre may be six or eight times that of the cambium initial in some species, in which the increase in number of cells should be correspondingly great. It is difficult to put this point to strict numerical test, because the limits of the developing tissue cannot be strictly defined, but if the broad band of undifferentiated tissue formed in the spring (Kostytschew [13, 14]) is compared with the fully differentiated wood, there is little indication that an increase in the number of elements in cross-section takes place which is comparable, in its extent, with the increase in length of the developing fibres.

Secondly, these elongated elements have elongated under compression at a time when their fluid contents contain little or no vacuolar sap, so that the change in shape is not likely to be associated with a reduction in volume. If the contents of the elongated cells remain the same, and if they slide past one another, then there will be no reduction in the total mass of these cells intervening between the vessels at any one level. All the pressure caused by the radial expansion of the vessels, therefore, will be thrown upon the cambium and it is difficult to understand why these fluid, plastic initials do not continue to deform and elongate, as they did in the Conifer cambium. These two points, considered together, suggest that the fibres have elongated without an equivalent increase of their numbers in cross-section, and without, therefore, sliding in amongst one another; and, further, that as a result, all the pressure of the radial expansion of the vessels is not taken up by the cambium on the periphery.

Finally, the question of corresponding pits requires examination. Upon Krabbe's hypothesis, in the spring wood, in which fibre elongation during development is practically universal, the walls of these fibres, which must have moved freely past one another as well as over the surface of the vessel, should show little or no correspondence of pits (*a*) between vessel and fibre, (*b*) between fibre and fibre. Actually, while pits often fail where vessel and fibre are in

contact, between fibre and fibre the correspondence is exceptionally good. But it will be as well to treat the question of pit correspondence between the different types of wood elements somewhat more fully, since these facts should be fully considered in any alternative method of regarding fibre differentiation.

The pits in the wood walls were most thoroughly worked out by Sanio (26, 27), and, though his terminology may require some modification to-day, his general results undoubtedly stand. Sanio distinguished four types of wood elements from one another.

1. *Wood parenchyma*. The fusiform initial, *whilst still meristematic*, divides into a series of cells by transverse divisions. The walls of these cells do not thicken greatly and they have simple pits; the protoplasmic contents are retained. A modification of this type is the *Ersatzfaser* ("substitution fibre"), in which the fusiform initial does not divide transversely, but when fully differentiated retains its protoplasmic contents with thin wall and simple pits.

2. *Wood fibres*, simple or septate. The fusiform initials do not divide transversely whilst in the cambium ring, the walls thicken considerably, and the protoplasmic contents finally disappear. During differentiation transverse septa may appear which may contain protoplasmic connections and ultimately fine pits or which may be quite smooth and uninterrupted. In any case these septa are thinner than the main walls of the fibre. Pits in the longitudinal walls of these fibres were described by Sanio as sometimes simple, sometimes bordered. They were correctly figured and described, but to-day we should call all these pits bordered, though the pit canal may lead in to a very flat, shallow cavity over the primary pit membrane. The pit canal is practically always slit-like in surface view.

3. *Vessel segments*. These types of wood elements are too well known to require further description. The wide pits are usually bordered, though the border may, in many cases, be very inconspicuous.

4. *Tracheids*. Strasburger's later classification of the elements of the wood (33) did not differ in essentials from that of Sanio, but he grouped them into two main classes, the tracheal and the parenchymatous. The tracheal elements included tracheae, tracheids and "fibre tracheids," the latter being in practice indistinguishable in many cases from "wood fibres" which were empty of contents. Strasburger regarded the "fibre tracheid," however, as always having bordered pits whilst the pits in the true fibre were always assumed to be without a border. Actually it is clear that

these elements grade into one another and it must be left for further consideration, in the light of a comparative study of development, whether a real distinction can be maintained between fibres of tracheal nature and fibres which, from development, should be regarded as homologous with parenchyma.

During development, the walls bordering these various types of elements may slide over one another. Parts of the walls of tracheids or vessel segments are often quite free from pits and apparently represent regions where such slip has taken place early; fibres frequently and parenchyma occasionally, when facing vessels, similarly show complete absence of pits on the wall in contact with the vessel. In other cases, pits may still be found in such walls facing one another, but may fail to correspond.

When slip does not occur on the other hand, then the "three-ply" wall of cellulose—middle lamella—cellulose, between two elements, must behave as one during any stage of cell extension. The result is that the pit membrane, even between dissimilar elements, is of equivalent size on both sides of such a wall, though the amount and nature of the secondary thickenings surrounding it will be characteristic of the type of wood element in which it is included. Thus, when vessel segment borders vessel segment or tracheid, the pits are usually largest, but if vessel segment borders parenchyma, the pits will be equivalent in size in both elements, larger than usual for the parenchyma element, if smaller than usual for the vessel. They will bear any usual border on the side of the vessel but will, as always, be simple on the side of the parenchyma cell.

In the rare cases where corresponding pits may be found between vessel and fibre, such pits are described by Sanio as relatively larger than usual on the fibre side, but smaller on the side of the vessel: the characteristic border and pore canal will be present in the fibre.

It is, however, characteristic of the fibres that whilst the pits almost invariably correspond where fibre faces fibre, they are frequently missing or fail to correspond where fibre faces vessel segment, tracheid or parenchyma. The correspondence of fibre pits with one another is best seen on examination of the wall in surface view, after appropriate staining. The slit-like pore canals of the two adjacent walls have a common spiral pitch, so that looking through the double wall they are seen to cross one another at an angle. If the pit membrane has been suitably stained, it will be seen as a circle which either includes the intersecting slits, if the pit membrane is wide, or is present as a small circle at the angle of intersection when

the slits are wider than the circular pit membrane (good figures in
Eames and MacDaniels(5), pp. 30–33, Figs. 18–22). Such corre-
spondence of pits between fibres is the very general rule and is
directly contrary to expectation upon the type of sliding growth that
is usually assumed to have taken place between such elements. In
old wood, an observation occasionally made, Text-fig. 12, suggests
that there may have been a slight lateral shift between the fibres as
they grew older. This point must be left for further elucidation; in
fully differentiated fibres in the young wood the correspondence
seems usually to be exact.
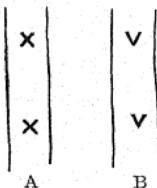
Text-fig. 12. Diagram of difference in correspondence of slits in the radial
walls of fibres, as seen in surface view, in young wood A, and in old wood B.
The appearance seen in B suggests some lateral slip without any vertical slip.
(From observations on *Acer Pseudo-platanus*.)

The alternative to sliding growth in fibre differentiation

As already suggested (24), the clue to vessel and fibre differentiation
is the early vacuolation of the future vessel element while still
amongst plastic, meristematic elements which are thus compressed
into long cells, subsequently to differentiate into fibres.

But the evidence just given as to the distribution of pits suggests
that the walls of this plastic tissue around the expanding vessel
element as a coherent system without slip between the
individual elements, and this process apparently takes place without
throwing strong radial compression upon the cambium. This must
mean that the movement of cell substance, brought about as the
result of the vessel expansion, is upwards or downwards in the axis,
and this result is only possible if the differentiation of the new vessel-
fibre system proceeds progressively up or down the axis. The seasonal
activity of the cambium will be examined in the next paper in this
series, where it will be shown that it seems to be the invariable rule,
in the hard-wood tree, that cambial activity in the axis begins each
spring below the buds and proceeds from thence downwards to the
roots. Similarly, later in the season, cambium activity ceases first at

the apex of the shoot, and this resumption of the resting condition
also takes place progressively downwards.

We may think then, without exception apparently, of the cambial
activity and vascular differentiation of the Dicotyledon axis as
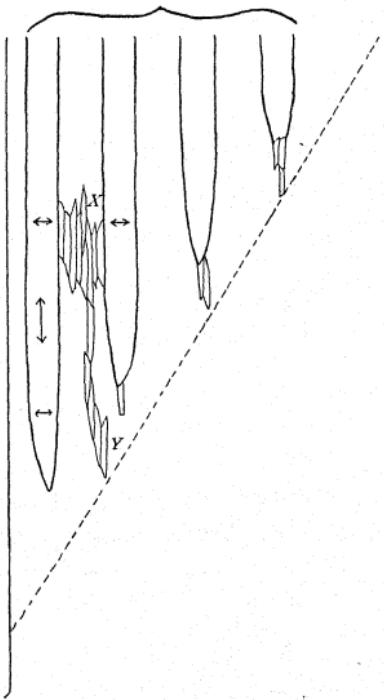
Text-fig. 13. Very diagrammatic representation of the wedge of newly
differentiating wood resulting from the progressive basi-petal resumption of
cambial activity. The vertical line on the left represents the surface of the last
year's wood, the active cambium is shown as a sloping interrupted line on the
right. The innermost vessel system in the new wedge has differentiated farthest
down: between it and the next vessel compression of the plastic elements has
proceeded much further (at X) than at Y where the plastic element is still in the
cambium layer.

proceeding in a wedge of tissue which is moving gradually down the
axis. Such a wedge is illustrated very diagrammatically in Text-fig.
13. The wide end of the wedge is the upper end. Here there is the
broadest band of new tissue formed to the inside by the cambium and
the largest number of new vessels have commenced to differentiate.

Each vessel system continues to differentiate downwards, the oldest system, differentiated furthest downwards in the wedge, lies to the inside, the shortest to the outside. As these vessel systems expand they compress the plastic network of cells between them.

But these cell systems, thus compressed, respond both by elongating and, in the case of the cells furthest away from the vessels, by displacement downwards. Upward movement is, of course, impossible, since the cells above are already compressed and elongated and are now probably in process of lignification. In the region, therefore, where these plastic cells are at the moment held between vessel segments within and without, the outer being in process of active expansion, the plastic cells will be elongating and, to some extent, moving downwards. But a little lower down, the elements to contribute to the outer and younger vessel will not yet be expanding. Here the cells, therefore, will be driven outwards by the expansion of the new segments added to the inner vessel, and the plastic cells, though not so compressed and elongated, will be to some extent compressed and driven outwards, a movement which will affect the plastic elements as far out as the surface of the cambium. We see, therefore, why the future fibres at X, in Text-fig. 13, are more elongated by compression than are the equally plastic cambium initials at Y.

Originally the cells at X were regular, symmetrical elements cut off from the cambium in radial rows. Their subsequent deformation under pressure is illustrated more in detail in Text-figs. 14 and 15. It will be seen that the change in shape to the elongated fibre initial can take place without necessarily any longitudinal slip at all. If such slip takes place, it is to be expected between vacuolated vessel and plastic fibre and will accentuate the movement downwards of the fibres. Near the expanding vessel, the original angles of the walls may be altered so that instead of the appearance shown in Text-fig. 14 at X, the point of union is carried by the downward movement of the cells further from the vessel on to a slope as at Y in Text-fig. 15.

Supposing that this movement occurs in a narrow group of plastic elements between two vessels, as in Text-fig. 15, the result may be to produce the re-entrant angle shown at the upper end of cell 3 in the lower row. This cell, on differentiation, will give rise to a forked fibre. In the actual observation of sections the outline of the compressed fibre initials are much harder to follow because the cells are relatively so much more elongated. Cell walls meeting on such sloping angles have often been seen, but only one or two clear cases

of such re-entrant angles have been found in section (Photos 3 and 4, Plate II). When, however, mature wood is macerated, forked fibres are fairly frequently found in the Dicotyledon. Thus, Sanio has described them for *Berberis vulgaris, Tilia parvifolia, Spartium scoparium, Vitis vinifera, Philadelphus coronarius, Euonymus latifolius, Quercus pedunculata, Ribes rubrum, Sambucus nigra, Artemisia abrotanum, Acer Pseudo-platanus, A. platanoides, Clematis vitalba, Amygdalus communis, Aesculus hippocastanum, Pelargonium roseum, Rhamnus frangula,* and says that he has observed them in other cases where he has not recorded the species. It is worthy of note that
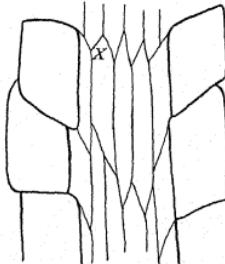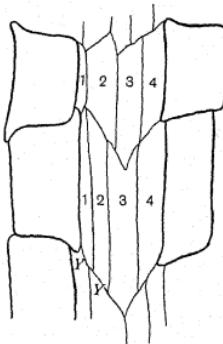
Text-fig. 14.   Text-fig. 15.

Text-fig. 14. Diagrammatic representation of the deformation of the plastic "fibre initials" between the expanding vessel segments.

Text-fig. 15. Plastic fibre initials deforming between expanding vessel segments. Cell 3 on the lower row will give rise to a forked fibre.

forked ends accompany this method of fibre differentiation, but are very rarely found, so far as the writer knows, in Conifer tracheids.

The only description of any similar structure in the wood of the Conifer known to me is the tracheid with V-shaped ends, figured by L. H. Dougherty (17) from macerated material of the wood of *Pinus radiata*. So far, no similar invagination of the wall of the fusiform initials near the apex has been seen in section through the cambium, and this apical invagination may arise during the subsequent differentiation of the tracheid from the fusiform initial. In any case there is no evidence of a vertical displacement of the whole framework of plastic walls in the Conifer cambium, such as takes place

when the plastic fibre initials are squeezed between the expanding vessels.

The fate of a "trabecula" (see p. 119), which may traverse the originally uniform meristematic tissue before vessel and fibre differentiation takes place, is worth brief consideration. The trabecula is stretched between the tangential walls of the vessel and as these move apart horizontally it retains its position, becoming thinner. In the fibre initials, the pressure upon the tangential walls, pushing them closer together, will hold the trabecula as a fixed point in this wall and the rest of the substance of the fibre initial will move downwards as it elongates without displacing the trabecula, which remains in line with the same structure in the expanding vessel. Of course, if an end wall of the fibre is carried into the trabecula by this vertical displacement, we may expect the trabecula to disappear, for being plastic wall material it will be reabsorbed into the wall, and this may explain the occasional absence of the trabecula, to which Nordlinger draws attention, as it runs through a series of wood elements. The slipping and distortion of the compressed cells, as they are driven apart by the expansion of the vessels on either side of them, may also cause the row of trabeculae, as seen in transverse section, to be distorted from their direct, radial path occasionally.

This method of mutual adjustment of the wall system of the future fibres accounts for the appearance of the elongated fibre without the necessity for any slip between fibre and fibre; it is, therefore, compatible with the almost invariable correspondence of pits upon their walls.

The transverse partition walls in the elongated wood parenchyma always remain practically transverse so that there seems to be no longitudinal displacement of the radial and longitudinal walls of these elements whilst they are plastic. In fact, it seems to be characteristic of such parenchyma, as of vessel segment or tracheid, that its vacuolation takes place relatively early, being accompanied in this case by cell division and the early formation of the transverse walls. As a consequence such parenchyma elements, if next to a vessel, do not undergo longitudinal displacement under pressure, but expand with it. Usually, therefore, the pits in vessels and parenchyma correspond, whilst for the same reason they frequently are missing or fail to correspond where parenchyma cell faces fibre. Correspondence may sometimes be found between fibre and parenchyma, as slip does not necessarily always occur. In particular, in the summer wood, especially in ring porous wood, all elements may

remain in continuous contact. The vessels have practically ceased to expand, the fibres as a consequence undergo no elongation, but remain equal in length to the cambium initials from which they are formed and all elements of the wood may then bear corresponding pits.

In the Conifer wood, the rays were regarded as fixed points, and similarly in the hard wood, in tangential section, the rays may be regarded as fixed points which undergo no longitudinal displacement, but which become gradually farther apart as the periphery of the cambium increases. In the hard-wood tree vessel expansion may actually distort the radial path of such a ray but in no case will such expansion force the ray cells apart from one another and interrupt a ray. On the other hand, as Krabbe pointed out, where vessel expansion is very great, as in *Quercus*, a ray may be forced so firmly up against the neighbouring ray, that the plastic fibre initials between them may be squeezed out of position and the cells of neighbouring rays brought into contact. Between these radially running, differentiated rays, the plastic fibre initials must also be driven downwards by the vessel expansion in the manner just described. The result will be, of course, that as a general rule pits fail to correspond between fibre and ray parenchyma, though correspondence between wood parenchyma and ray parenchyma is common and correspondence is also found between ray parenchyma and vessel or tracheid. Furthermore the downward movement of such plastic fibre initials will sometimes force the ends of these elements right against the upper surface of such a ray; usually the fibre elements will slide laterally round to right and left, but occasionally they may fail to do this. Grossenbacher has figured such a case in apple, where the ends of the fibre initials are seen to be curved along the top of the ray (7). Such a result seems evidence rather of the passive distortion of plastic fibre initials, thrust against the unyielding surface of the vacuolated cells of the ray, than evidence of the "sliding growth" of the points of such fibres.

DISCUSSION

In the cambial activity of both soft-wood and hard-wood tree, the readjustment of cell position during cambial growth and xylem differentiation has now been closely examined, special attention being directed to the formation of elongated fusiform initials in the soft-wood tree and elongated fibres in the hard-wood tree, in each case in an axis which has ceased to grow in length. In both cases it

appears that the process usually assumed, the sliding growth of the points of the elongated cells past one another, is very unlikely to occur and is not easily reconciled with the distribution of the plasmodesma and pits in these elongated cells and the elements to which they give rise. This "sliding" type of growth has always been hypothetical, but has been universally accepted because of the lack of any alternative method to account for the readjustments of cell position which could be seen to be taking place during tissue growth and differentiation.

In the previous pages, such an alternative account of growth and differentiation in the developing wood of trees has been put forward. It also is only a hypothesis, but it is much more compatible with the distribution of the pits in the walls of the adult tissues, and also makes some of the cell shapes, such as forked fibres, etc., much more readily intelligible. The writer has no doubt whatever that this alternative method of regarding cambial growth and xylem differentiation represents much more closely the actual processes which occur, as these complex tissues change in size and readjust the mutual position of their constituent cell units. Unfortunately it is, perhaps, a process which is a little more difficult to grasp than, on the surface, the hypothesis of sliding growth appears. It also lacks a convenient single descriptive phrase, to define its characteristics and to set it in opposition to the hypothesis of "sliding growth" (or "gliding growth"), which has now gone almost unchallenged for more than forty years.

It is proposed to call this alternative method of growth now described *symplastic growth*. It is suggested that this mode of growth is characteristic of meristematic tissues, whether they form part of an apical growing point or an intercalary cambium. In this method of growth, mutual adjustment of cell position takes place between semifluid protoplasts, separated from one another by plastic walls, which move as a common framework under tension and without any slip between the wall surfaces of neighbouring cells. This method of visualising cell adjustments in a growing tissue seems remote from the usual botanical standpoint. It has, however, been very fully discussed and recommended to the botanist by D'Arcy Thompson [36] in his book upon *Growth and Form* (pp. 304 *et seq.*). Probably the reason these suggestions have been so disregarded by botanists is the general impression that the data are fully and adequately covered by the concept of sliding growth. When this was shown not to be the case, a full examination of the possibilities of "symplastic growth,"

in relation to the peculiarities of radial growth in trees, was obviously indicated.

Now that such a re-examination of these phenomena has been carried out, the writer realises that the original stimulus, which impelled him to carry out this task, was probably conveyed in a private letter from Professor D'Arcy Thompson, which drew his attention once again to the significance of tensions in the cell walls in connection with the outlines adopted by living, dividing cells. Probably such a standpoint is more readily grasped by the zoologist; the botanist is too much impressed with the constraining effects of the thick, semi-rigid cellulose wall, which separates the living protoplasts in the *adult* tissues of the plant.

In this paper Krabbe's original suggestions as to sliding growth have only been under examination so far as cambial activity and wood formation are concerned. But if the position taken up is correct it is clear that all other facile generalisations as to the occurrence of sliding growth require re-examination. In particular, wherever plastic, meristematic cells give rise to elongated elements with pointed ends, such changes are little likely to be associated with the sliding of such elements past one another. Thus on the face of it, in the differentiation of the secondary bundles of *Dracaena*, or indeed in the differentiation of any Monocotyledon bundle, examination shows corresponding pits upon the fibre tracheids and indicates that slip has probably occurred not between these individual elements, but between their walls when plastic and those of the surrounding vacuolated cell sytem. Similarly, Tammes' objections to the sliding growth of primary bast fibres will probably be found to have validity (34). In this case we may actually have the lower end of the fibre wall undergoing thickening and held firmly amongst fully differentiated elements whilst the upper end, in an internode which has not yet ceased to grow in length, is still elongating under compression (Aldaba(1)). Here again slip, if it occurs, should be found between fibre and surrounding parenchyma rather than between fibre and fibre. Obviously this standpoint opens up a large field of developmental anatomy to a re-examination which will have its repercussion upon the reception of the hypothesis as to the growth of meristematic tissues which is contained in these pages. At the moment it must suffice to indicate the wide scope of the issues raised and, in conclusion, to point out that the new standpoint seems to harmonise much better with general experience as to the behaviour of the cambium as a meristematic layer.

This may best be illustrated by dealing with two specific cases, (1) the "branch crotch" and (2) certain ringing experiments which have been the subject of Rumanian observations.

(1) The "branch crotch"

Very often the upper angle between branch and main axis, or between two branches, forms a surface which diminishes in area with each year's increment of wood. As a result the older layers of bast are of greater superficial area than the wood surface which has to accommodate them and are thrown into folds upon the wood. The cambium, on the other hand, continues to adjust itself perfectly to this diminishing surface: part of it seems to move round the flanks, where the surface is increasing with increase in radial increment, the individual cambium initials growing smaller and more isodiametric and as a consequence the vessel segments or tracheids formed in the wood becoming shorter in the crotch. Such smooth adjustment of the cambium to the changing surface is to be expected if the layer consists of semi-liquid protoplasts, with plastic walls. The fusiform initials in the crotch will be under diminishing tension and will grow shorter. With this reduction in length they will decrease in mass, because, after cell division, the proportion of surface to mass will adjust itself in accordance with the diminishing surface. In such a "branch crotch," or at any irregular surface of the living wood, therefore, the semi-liquid protoplasts of the meristematic cambium form a layer which will adjust itself perfectly to the irregularities of the surface and to the changing pressures and tensions in the system thus produced.

(2) Ringing experiments

Teodoresco and Popesco have described the result of the anatomical examination of a strip of bark, such as is represented at A, B, C in Text-fig. 16, which has been left as a bridge across a ring in accordance with the experimental practice first introduced by Czapek. In such a strip they found after some months' growth that the new xylem and phloem at B had the long axes of the cells lying horizontal whilst they were still vertical in the strip at A and C (35). The same change of orientation was observed in rings in both Dicotyledons and Conifers.

These changes in cell shape in the strip at B are obviously a record of the changes in shape of the cambium cells from which the new tissues are derived. These changes have recently been followed in detail by Miss R. M. Tupper-Carey, and will be described in a

separate communication; they are readily intelligible from the standpoint developed in this paper. After the ring has been made, the first change is that practically all the cells in the region of the cambium become isodiametric as viewed in tangential section. Thus, the fusiform initials divide up to form isodiametric cells, as has also been observed by Bailey when stems containing long fusiform initials are cut. When cambial activity begins again under the bark in the bridge across the ring, a number of these isodiametric cells again behave as plastic, meristematic cells and deform under pressure. This strip of bark will be held firmly down to the exposed surface of the wood by dried, suberised exposed tissues, and by cork, so that it cannot be raised by the formation of the new secondary tissues underneath without putting the plastic cells in this tissue under
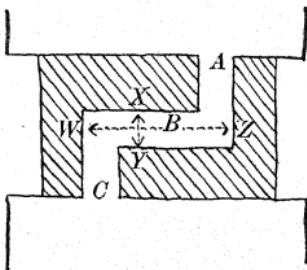
Text-fig. 16. A ring according to Czapek's method, with strip of cambium left running across the ring at *A*, *B*, *C*.

pressure. The result is that these cells elongate symplastically once more, but now, in the transversely running portion of the bridge at *B*, the direction of elongation is transverse to the axis of the tree. The relative changes in the shape of the fusiform cells in the cambium at *B* during this period are indicated in Text-figs. 17 A, B and C.

The reason for the transverse elongation of these initials in the transverse portion of the bridge will be more fully discussed elsewhere, but this change is obviously taking place in plastic cells by a process of symplastic growth. In each new series of tangential divisional walls, the new orientation is progressively adopted and throughout this time the transverse and radial walls of these cells are gradually adjusting themselves to the new tensions. As radial growth proceeds in this strip, there will be slightly more space for growth in a transverse direction, because the strip of cambium forms an arc upon the surface of the wood, of which the radius is increasing.

The main factor, however, in causing the transverse elongation of
the cells of the cambium in the transverse strip is probably the fact
that cambial activity recommences gradually in the bridge, starting
in A and then moving gradually across B, from right to left, before
passing down C (Text-fig. 16).

Under the horizontal strip of bark, the rays, as seen in tangential
longitudinal section of the new tissue, are somewhat irregular; they
are wider than usual and the long axis of the ray is not so definitely
and universally in accord with the new direction of the long axis of
the fusiform initials. None the less, they are evidently changing in
orientation, and such a change can only be brought about by a
double process. The original vertically extended rays must be broken
up by occasional cells in the ray, in the cambial region, reverting to
the meristematic condition and then becoming fusiform initials with
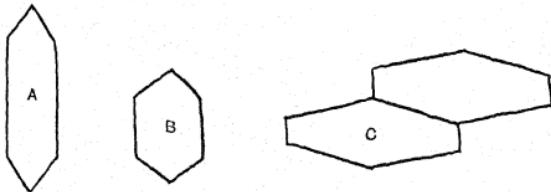
Text-fig. 17. A–C. Diagrammatic representation of the general changes in
shape of the fusiform initials in the strip of cambium at B in the ring (fig. 16). A
shows original shape, B the transitional stage and C the shape attained as
radial pressure increases with renewed growth.

the new orientation. Then the new rays arise through fusiform
initials, with the new direction of extension, breaking up entirely or
in part into ray cells, which then lie in rows that are at right angles to
the vertical axis of the tree. Similar observations on the breaking up
of rays, which can be interpreted in the same manner, are made by
Jost [10] and Neeff [20].

It is clear that a whole series of growth phenomena in the cambium
will ultimately require re-examination from this standpoint, in
particular the obscure phenomenon of spiral grain. These two
examples are only cited to show how very suggestive the new stand-
point appears to be in relation to phenomena which up till now have
certainly seemed very inadequately elucidated.

SUMMARY

The nature of the fluid protoplasts of the apical meristem, with plastic walls interpenetrated by protoplasmic connections, makes it difficult to visualise adjustments in cell position in such a tissue as occurring by slip between the walls of neighbouring cells.

Furthermore such slip would rupture the plasmodesma, which, once broken, are very unlikely to be rebuilt. Pits are found, in thickened walls, in the regions originally penetrated by plasmodesma, so that if walls slide over one another during development no pits will be found in them subsequently, or the pits present will not correspond in position in adjoining cells.

Adjustment of cell position in the apical meristem is possible, without slip between the cells, by mutual mass readjustments between the semi-liquid protoplasts, accompanied by a movement of the whole framework of plastic walls under tension.

Movements of this type adequately explain the adjustments in cell shape and cell position that take place as the isodiametric meristematic cells present in the apical meristem multiply by division and gradually change, in the procambial strand, into elongated procambial and cambial meristem cells.

These cambium cells are elongated in a longitudinal direction because, as they are compressed radially, the repeated transverse divisions of the parenchymatous cells around them, and their continued longitudinal extension, provide ample space for the extension of the compressed meristematic cells in a longitudinal direction.

In the Conifer, however, the fusiform cambium initials continue to increase in length for many years although the elongation of the stem in length has ceased. This increase in length takes place in spite of the occasional transverse division of these fusiform initials. The changes in cell form and position involved in these growth processes have usually been explained as due to the sliding growth of the fusiform initials. This explanation is examined and found to be at variance with known facts as to the distribution of plasmodesma and pits in the wood and phloem cells differentiating from the cambium. The same changes in cell shape and position could be brought about in such a meristematic tissue by readjustments of fluid protoplasts and plastic walls of the type already described for the apical meristem; the framework of walls then adjusts itself continuously as a whole, without slip on the radial walls between the individual meristematic

units. This method of cell adjustment, for which the term *symplastic growth* is suggested, is shown to be more consistent with the subsequent distribution of pit and plasmodesma connections.

The straight outward radial path of a trabecula traversing a series of tracheids, the cambium and the phloem elements, is also compatible with this method of cambial growth.

In the hard-wood Dicotyledon, after the first year, fibres elongate from cambium initials in a tissue in which extension in length as a whole has ceased. This has also been put down to sliding growth, but whilst slip certainly takes place between the wall of the vacuolating vessel and some of the elements around, groups of fibres probably elongate as a common system without any slip between the individual fibres constituting the group.

It is shown that the adjustment of cell shape and position, occurring in the plastic cells between the expanding and downwardly differentiating vessels, accounts for the development of the fibres and for the relatively great length of the fibre compared with the length of the less compressed cambium initial from which it is derived.

It is pointed out that all instances where sliding growth has been postulated between the individual units of a meristem are under suspicion and deserve re-examination.

In so far as the cambium is concerned, the new standpoint seems to provide a much more intelligible conception of the manner in which the growth of the cambium adjusts itself to the changing conditions, such as are found for instance in the crotch of a branch, or produced under a strip of bark left as a bridge between the lower and upper edges of a ring.

discussed these problems with him. Out of one such discussion has come the term "symplastic growth," which was originally suggested to him by Mr W. Wight, B.Sc.

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DESCRIPTION OF PLATE II

Phot. 1. Longitudinal tangential section of the cambium of *Pinus sylvestris*. The nuclei are showing in the section, whilst the uneven thickening of the radial walls is prominent in some cases. (× 131.)

Phot. 2. Longitudinal tangential section of the wood of *Pinus sylvestris*. The cells at the ends of the rays have fully lignified walls, whilst some of the inner cells of the ray have wide pits. (× 131.)

Phot. 3 and Phot. 4. Longitudinal tangential sections of the wood of *Acer pseudo-platanus*. Phot. 3 (× 341) is in the region of the cambium. In both photos an element is present which might be expected to give a forked fibre on maceration. In Phot. 4 (× 333) this element is close against the top of the ray in the centre of the photograph.

Phot. 1

Phot. 2

Phot. 3

Phot. 4

PRIESTLEY—STUDIES IN THE PHYSIOLOGY OF CAMBIAL ACTIVITY
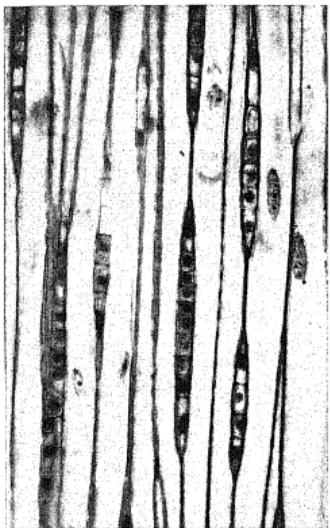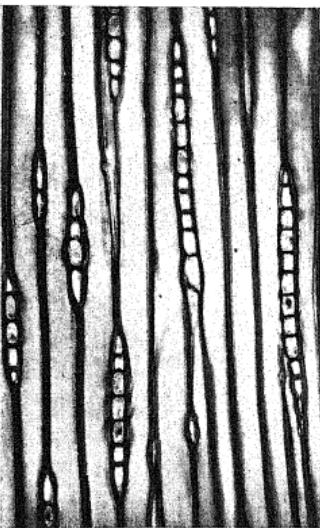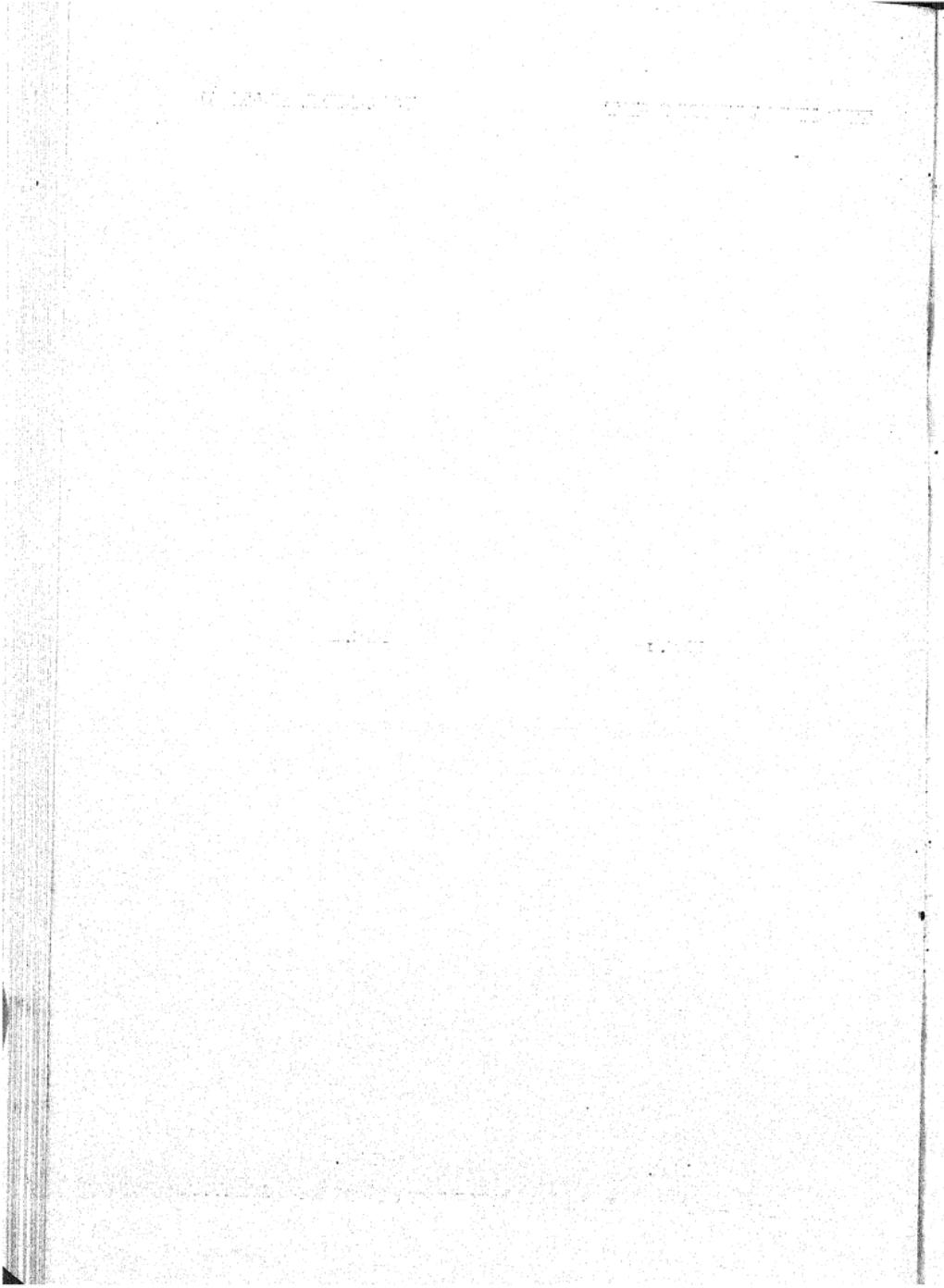
THE DISCOVERY OF *OEDOGONIUM PRINCEPS* (HASSALL) WITTROCK IN NORTH AMERICA

By GWEI-SZE MON-CHEN WU
AND JOSEPHINE E. TILDEN

University of Minnesota, U.S.A.

(With 15 figures in the text)

A STUDY of the literature makes it clear that *Oedogonium princeps* (Hassall) Wittrock has been found in only two localities in the world, one "near Notting Hill, in the vicinity of Cheshunt, England," and the other "in Glenwood Park, Minneapolis, Minnesota." In 1842 it was collected and described from its English habitat. Its discovery in Minnesota in 1922 and again in 1927 seems a curious phenomenon.

REVIEW OF LITERATURE

In 1842 a new species of green alga was described by Hassall ((4), p. 388) under the name *Vesiculifera princeps*. On the following page a second species was described, *V. capillaris* Linnaeus. This is said to be "very abundant in ponds in the brick-fields near Notting Hill; it also occurs occasionally in the vicinity of Cheshunt." In footnotes the author shows that he is in some doubt, but suspects that the two are the same species.

Three years later, on p. 195 of his *History of the British Fresh-water Algae*, Hassall (4a) repeats the second description under the specific name of *V. capillaris* Hassall, and again gives "Ponds near Notting Hill; Cheshunt, and its vicinity," as the habitat and locality and "A. H. H." as collector. The form is now illustrated by two figures which are copied for this article. The first figure (see Fig. 12*) probably represents a male plant. The basal cell is somewhat swollen and the apical cell characteristically rounded, while the whole figure looks very much like Minnesota specimens which are unquestionably male plants. The second figure (see Fig. 13) is a fairly good drawing of a female plant with a basal holdfast cell and two oogonia containing mature oospores. The oogonia occupy the position of the third and fifth cells of the plant, but strangely enough they each display *six* "caps."

No further mention is made of the material collected by Hassall for thirty-two years. In 1874 Wittrock (6) published the *Prodromus*

Monographiae Oedogoniearum, and on p. 42 of this one finds "*Vesiculifera princeps* Hassall" and "*V. capillaris* Hassall" both included under the name "*Oedogonium princeps* (Hassall) Wittrock." In a footnote Wittrock states that he has seen the original material of Hassall from the herbarium of Professor J. E. Areshoug. His
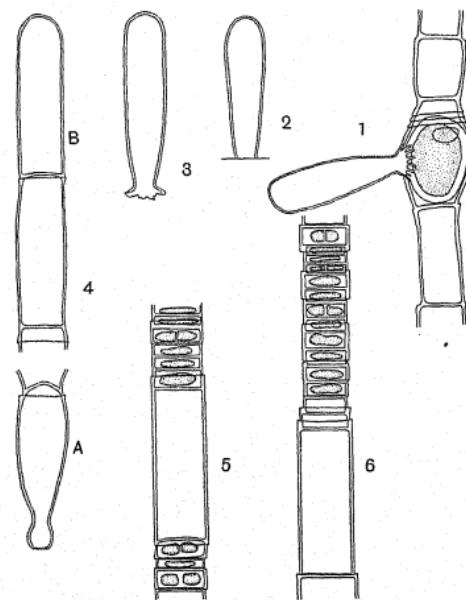
Figs. 1–6.

1, 2, 3. Young male plants attached to older *Oedogonium* filaments. (× 200 diam.)

4. Basal and terminal portions of a young five-celled male plant. (× 200 diam.)

5, 6. Vegetative and antheridial cells of mature male plant. Vertical division of sperms is shown. (× 200 diam.)

description of the material is carefully worked out, and, for the first time, accurate measurements are given, at least, for the female plant. No mention is made of the male plant. Under "habitat" is the bare statement: "In Britannia, Lusitania." (Lusitania is a name for Portugal. Wittrock includes a specimen, No. 109, from Welwitsch's *Phycotheca Lusitanica*, under *Oe. princeps*.)

Cooke's [2] *British Fresh-water Algae*, published in 1882–1884, contains an exact translation of Wittrock's description of *Oe. princeps* and includes both the *V. princeps* and *V. capillaris* of Hassall. No locality other than "England" is mentioned. However, Cooke must have examined Hassall's herbarium material, for he gives, on Plate 65, three figures, 2, 2 and 2 A, which are extremely
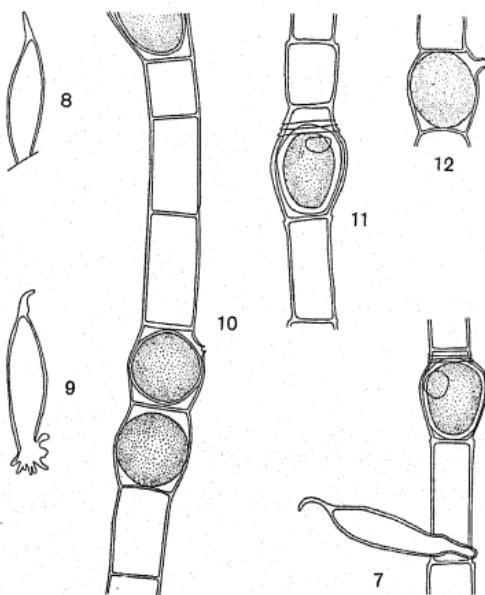
Figs. 7–12.

7, 8, 9. Young female plants attached to older *Oedogonium* filaments. (× 200 diam.)

10, 11, 12. Vegetative cells and oogonia of mature female plants. (× 200 diam.)

helpful in the study of the history of this species (see Figs. 14 A, B, C). Fig. 2 A (14 C) is without doubt drawn from antheridial material of *Oe. princeps*, though only three cells are shown.

De Toni [3] in *Sylloge Algarum* (1, 81, 1889) repeats Wittrock's description of *Oe. princeps*.

Finally, Hirn [5], in 1900, describes the species with much greater thoroughness than had been done before, and he presents four original drawings from the English material, these representing

several oogonia, a basal cell, and an apiculate end-cell of a female plant. He says: "Um dies mit Gewissheit zu entscheiden wäre es jedenfalls nötig die Antheridien von *Oe. princeps* zu kennen. In dem Originalmaterial waren keine vorhanden" (p. 290). Cooke's drawing of the three-celled fragment of a compound antheridium was apparently overlooked by Hirn, or, more probably, he felt unwilling to describe what he had not personally observed. Hirn examined Welwitsch's specimen, No. 109, and pronounced it to be not *Oe. princeps* as Wittrock had considered it. He restricts the distribution of the species to the original locality in England: "Britannia: ad Notting Hill prope Cheshunt Angliae (Herb. Wittrock. Leg. cl. A. H. Hassall)" (see Figs. 15 A, B, C).
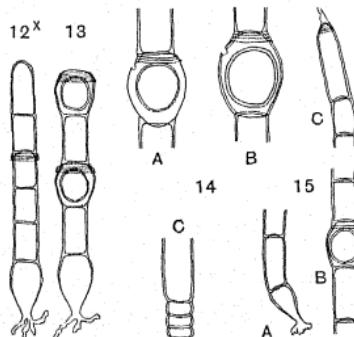
Figs. 12*–15.

12*. Young male plant (?). (After Hassall.)

13. Female plant with oogonia. (After Hassall.)

14 A, B, C. Oogonia and antheridial cells (?). (After Cooke.)

15 A, B, C. Portions of female plant, showing basal cell, one oogonium, and apiculate apical cell. (After Hirn.)

OEDOGONIUM PRINCEPS IN MINNESOTA

In Glenwood Park, in the city of Minneapolis, there has been constructed an artificial waterfall, known as Loring Cascade. It is set in a hill and apparently consists of large boulders of water-worn granite, but in reality it is built of gravel, sand, small rocks and iron wire cemented together in a clever manner. Water is kept running over the falls daily from May till October, it being turned on in the morning and off in the evening. It passes over the several ledges in the falls and then runs back into Glenwood Lake in a stream called

Cascade Stream. Loring Cascade, built in 1917, is an interesting feature in physical geography. Here one is able to observe an algal flora in course of formation.

A taxonomic study of the algal flora of Loring Cascade was made by Sister Emmanuel Woolsey during the years of 1917 and 1918, and in the year of 1922 she carried on an ecological study of the algae growing in the various pools and falls of Cascade Stream. During the year 1922 Sister Emmanuel collected, on seven different occasions, a species of *Oedogonium*, represented by male and female plants with antheridia and oogonia. The plants were found, for the most part, in "First Pool" of the Cascade, and some of them in Cascade Stream. These plants were easily traced to Hirn's *Oe. princeps*, but due to the fact that the male plant of that species had never been described a good deal of doubt was felt, and finally some material was sent to Dr Transeau to ascertain whether he had ever met the form in his work on the Oedogoniaceae. Dr Transeau without hesitancy pronounced the specimen to belong to *Oe. princeps*.

During the first week in April, 1927, Miss Wu began a study of the algae of Loring Cascade. She also collected in a near-by pond, "Cat-Tail Pond," which is a shallow pool about 150 feet in diameter, in all probability fed by springs. The country around the Cascade and pond is hilly, the "hills" being terminal moraines. During the period of eight months, from April to November, collections were made weekly. Soon after the November 13th collection was made, the water froze and the work had to be discontinued.

In the material collected on April 5th, 1927, there appeared a three-celled *Oedogonium* plant—later proved to be a young male plant of *Oe. princeps*, because of the typical rounded terminal cell. After that sterile plants were found in abundance. During the first two weeks of August, female plants occurred, with oosperms, and male plants were likewise plentiful. At this time it was possible, without much trouble, to place the female plants under the species *Oe. princeps* (Hassall) Wittrock, according to the description given by Hirn, but as the male plant of that species had never been recorded—as far as known—some doubt was still felt in including it here without making another attempt to gain additional information as to the possible distribution in the United States. Since Dr Tiffany had recently published a paper on the Oedogoniaceae of this country, some specimens and drawings were sent to him. Dr Tiffany thought the material very interesting, though puzzling, but believed it to belong with *Oe. princeps*.

The authors present the following revised description of the species *Oe. princeps* (Hassall) Wittrock:

Oedogonium princeps (Hassall) Wittrock char. emend. Hirn, K. E., *Monographie und Iconographie der Oedogoniaceen*, pp. 289–290, Pl. 10, fig. 56, 1900.

> *Vesiculifera princeps* Hassall. *Ann. and Mag. Nat. Hist.* 10, 388 (ex parte), 1842.
>
> *V. capillaris* Hassall. *Hist. British Freshwater Algae*, 1, 195; 2, Pl. 50, figs. 1, 2, 1845.

Oedogonium princeps (Hassall) Wittrock. *Prodromus Monogr. Oedogoniearum*, p. 42, 1874; Cooke, *British Fresh-water Algae*, 1, 171; 2, Pl. 65, fig. 2, 1882–1884; De Toni, *Sylloge Algarum*, 1, 81, 1889.

Oe. dioecious, macrandrous; oogonia single or occasionally in groups of two, slightly swollen, somewhat oboviform, opening by a superior pore; oosperms globose or subglobose, not filling the oogonium, with a smooth membrane; terminal cell of the female plant apiculate; male plants slightly wider than the female; antheridia 2–33-celled; sperms two, with division vertical; basal cell somewhat elongate, a little swollen; terminal cell of the male plant obtuse, rounded.

Female plant:

Veg. cells	34–39 ×	38–155 mic.
Oogonia	51–56 ×	54– 77 ,,
Oosperms	47–54 ×	47– 65 ,,
Young plants	26–30 ×	108–135 ,,

Male plant:

Veg. cells	38–43 ×	64–141 mic.
Antheridial cells	34–38 ×	5– 13 ,,
Sperms	3– 6 ×	8– 10 ,,
Young plants	30–35 ×	116–142 ,,

Floating in pools and attached. In Cascade Pool and Cascade Stream; and in Cat-Tail Pond, Loring Cascade, Glenwood Park, Minneapolis, Minnesota. Sister Emmanuel, 1922; Gwei-sze Wu, 1927.

A table has been prepared to allow of comparison in the matter of the time of producing oogonia and antheridia.

	1922	1927	Cat-tail pond	First pool	Cascade stream	D pool	*x* sterile plants	*y* male plants	*z* female plants
April		5	+y (1)					+	
June		8		+x			+		
,,		16		+x			+		
,,	24			+z			+		+
,,		25		+x			+		
July	1			+y (2)			+	+	
,,		2	+x				+		
,,		9	+x				+		
,,	11			+z			+		+
,,		17		+x			+		
,,	25				+y (2)		+	+	
,,		30		+x			+		
August		6	+yz				+	+	+
,,		13	+yz	+x			+	+	+
September		3		+x			+		
,,		10	+x				+		
,,		17	+x	+x			+		
,,		24	+x	+x			+		
,,		30		+z			+		+
October		1	+x	+x			+		
,,		8		+x			+		
,,	9			+y (2)				+	
,,	14			+y (2)				+	
,,		15		+x			+		
,,	21					+y (2)		+	
,,		22	+x	+x			+		
,,		31		+x			+		
November		6	+x	+x			+		
,,		13	+x				+		

Sterile plants	... ...	*x*
Male plants	... ...	*y*
Young male plants	... ...	*y* (1)
Antheridial plants	... ...	*y* (2)
Female plants	... ...	*z*

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(6) WITTROCK, V. B. *Prodromus Monographiae Oedogoniearum*, p. 42. 1874.

(7) *WOLLE, F. *Fresh-water Algae of the United States*, **1**, 93–94; **2**, Pl. 78, fig. 3. 1887.

* Wolle includes a description of *Oedogonium princeps* (Hassall) Wittr., curiously enough from "Minnesota, near Minneapolis." The collector's name is not given. But Collins places this under *Oe. capilliforme* var. *australe*.

REVIEW

Recent Advances in Plant Physiology. By E. C. BARTON-WRIGHT,
  M.Sc. With a Foreword by Professor R. RUGGLES-GATES, M.A.,
  Ph.D. London: J. and A. Churchill, 1930. Pp. xii + 352, with
  51 figures in the text. Price 12s. 6d.

In this book there are made available the fruits of a wide reading in modern
plant physiology. The effort has been to select and discuss "important and
fundamental papers published in each year of the last decade," and it will
readily be agreed that the great majority of the publications touched upon
justify their selection. In most cases the author has been content to report
results and the conclusions arrived at by the original workers, but in a few
instances theories are described in order to be discredited. In the case of the
hypothesis concerning the ascent of sap, which is so treated on pp. 110–114, it
is doubtful whether this was worth doing again.

The book has unfortunately been seriously handicapped at the start, both
in its title and preface. The former is a little misleading, for in spite of the
declaration that the "text covers a strictly limited period; approximately the
years 1918–1928," references to the two previous decades are frequent, and
these would not usually be considered recent in so young a subject. Some such
title as "Some Aspects of Plant Physiology Reviewed for Students" would have
been more descriptive, but no doubt the author was not a free agent in this
matter, the book being published in a series. The preface does the book more
serious disservice. It states that "economic aspects" have been stressed, since
research for its own sake is no longer considered an adequate object, and that it
is only by exploiting economic interests that the subject can be advanced.
This view appears extreme, and even forbidding, but in fairness it must be
said that an exploration of the text leaves the reader unaware of the declared
bias.

The author hopes that the book will fill the gap at present left by the
absence of any "adequate text-book, which covers the ground necessary for
students reading for their final honours degree." Considered from this stand-
point, certain omissions and assumptions become serious. Little is said, for
example, of the large amount of continental work on various aspects of irrita-
bility, other than the conduction of stimuli. A complete knowledge of the
chemistry of sugars is assumed, though proteins are given nearly a dozen pages.
It is also assumed that the meaning of "organisation resistance" will be
apparent merely upon mention, whereas the present writer's experience is that
students find this concept distinctly troublesome. On p. 215 the effect of many
factors upon the rate of respiration is dismissed as "too well known to be
considered here"; fair enough, perhaps in describing recent advances, but
decidedly high handed in a general text book. The important work of Maximov
presumably appeared too late for inclusion, but much more would be required
concerning the action of enzymes.

There are times when the author appears illogical, as for example, a quite
inexplicable "therefore" on p. 149, and the phraseology is sometimes slipshod,
as in the "curves very similar to Harder." These may be venial faults in a
technical handbook, but are more serious in a book intended for students,
whose principal effort must be to attain clarity of thought and expression.
Perhaps the most serious shortcoming from this standpoint is, however, the
absence of any attempt to develop the subject as a whole, or to bring out
underlying principles. A certain number of interesting aspects have been
dealt with, and that is all.

There are a few misstatements of fact. Glycolysis, as defined by Blackman, is not similar to the conversion of hexose into ethyl alcohol and carbon dioxide in yeast, but to the first stage in this process (p. 214); the alternative to a broken curve for photosynthetic rate is not necessarily a logarithmic one (p. 144); and for the theory of the interaction of factors, it is at least as important to determine whether the curves as usually plotted coincide at low values of the variables as to decide their shape. Davis, Daish, and Sawyer did not always find sucrose to be in excess of hexose in the leaves of the mangold (p. 157), but only in the summer.

To bring together so much that is scattered cannot fail to be of great service to students of the subject, and, moreover, at the moment of publication, the work is almost journalistic in its reporting. A well-selected list of references is attached to each chapter, which will be useful in starting the budding specialist upon the bibliographical trail. There is also an adequate index, and abundant graphical illustrations drawn from original papers.

W. O. JAMES.

SYSTEMATIC ANATOMY OF WOOD

O<small>N</small> the occasion of the Fifth International Botanical Congress, to be held at Cambridge from August 16th—23rd, 1930, it is proposed to hold an informal conference on the Systematic Anatomy of Wood. The subject is rapidly increasing in importance, particularly in relation to the identification of timber. The numerous anatomical descriptions of timbers, which have been published of recent years, direct attention to the lack of any standard terminology, and it is thought that the Congress will provide a unique opportunity for discussing the possibility of introducing some measure of standardization, at least among English-speaking people. If sufficient support were forthcoming, it might prove desirable to appoint a standing committee to collate the views of workers in this field and to issue recommendations for general adoption.

It is also hoped to arrange a scheme for the exchange of material among botanists and forest botanists who are willing to undertake the study of a family or group.

We are desirous of obtaining the views and co-operation of as many as possible of those who are interested in this subject, and we therefore invite suggestions of matter for discussion both from botanists who propose to attend the Congress and from those who will be unable to do so.

We hope that you will be so good as to bring this letter to the notice of any of your colleagues whom it may concern and who may not receive a copy.

<div style="text-align:center">

L. CHALK (Imperial Forestry Institute, Oxford).

S. J. RECORD (Yale School of Forestry).

B. J. RENDLE (Forest Products Research Laboratory, Princes Risborough).

</div>

I<small>MPERIAL</small> F<small>ORESTRY</small> I<small>NSTITUTE</small>,
  U<small>NIVERSITY OF</small> O<small>XFORD</small>,
    February, 1930.

LABORATORY NOTE

LACTOPHENOL AND COTTON BLUE STAINING
FOR MICROTOME SECTIONS

SINCE the introduction of the microtome into mycological technique, a number of attempts have been made to devise a successful method of staining microtomed sections of fungal hyphae in non-woody plant tissues. Innumerable stains have been tried for differentiating between parasite and host, and undoubtedly a combination of lactophenol and cotton blue is one of the best stains for general work. This gives excellent results with hand sections and bulk material, the lactophenol rendering transparent a considerable thickness of tissues. With microtomed sections, however, there has always been the difficulty of heating up the slides in lactophenol without detaching a considerable number of the sections. To eliminate this loss, the writer has found the following method very useful with various Peronosporales, Erysiphales and Uredinales parasitic in leaves and non-woody stems:

Instead of the normal viscous lactophenol solution, use throughout the staining process a solution of this diluted with an equal volume of methylated spirit. Shake thoroughly before use, to ensure proper mixing.

Bring sections to 50 per cent. alcohol. Place the slides in a deep Petri dish, large enough to accommodate a single layer of a convenient number of slides to be stained. Pour in the lactophenol diluted with methylated spirit until the slides are completely immersed. Warm slowly on a copper stage, covering the dish, but allowing for the escape of vapour. Continue heating for a few minutes after the alcohol has started to vaporise. Cool, and transfer the slides to a similar dish of cotton blue in lactophenol, the normal solution diluted as before with methylated spirit. Re-heat as previously. Cool, drain off excess of staining fluid and place in smaller dishes of lactophenol diluted with methylated spirit. Shake slightly and heat again.

After cooling, the sections can be examined under a microscope without taking the slides out of the dishes. If the fungal hyphae are not sufficiently stained, take the slides back to cotton blue and heat for a longer period. Wash out excess of stain by heating in a series

of dishes of lactophenol diluted with methylated spirit. The same series and staining solution can be used for several batches of slides if from time to time methylated spirit or preferably 90 per cent. alcohol is added to keep up the approximate original concentration, thus preventing the liquid from becoming too viscous.

When the washing is complete, the slides can be taken up from 50 per cent. alcohol to a permanent mount in Canada balsam. But the hyphae and host structures are much more clearly defined when the sections are mounted in lactophenol, and thicker sections, showing better continuity of hyphae, are rendered more transparent. In this case, drain off the alcoholic mixture and replace with ordinary lactophenol, or warm the slides on the copper stage so that the alcohol and water evaporate off before the coverslip is put on.

By the use of this method the whole of the microtomed sections can be kept on the slides during the staining process.

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THE

NEW PHYTOLOGIST

THE ARBORESCENT HABIT IN ANGIOSPERMS

A REVIEW

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(With 17 diagrams in the text)

CONTENTS

I. INTRODUCTION

THERE has, for a number of years, been much speculation as to the origin and characteristics of Primitive Angiosperms. The chief points under discussion are concerned with:

(1) The ancestral forms from which Primitive Angiosperms may have evolved[1], either mono- or polyphyletically, and

(2) The conditions which favoured their evolution[2].

(3) The habit of Primitive Angiosperms, whether arborescent or herbaceous[3].

(4) Their stem structure, and the presence or absence of a cambium[4].

[1] Arber and Parkin(8,9); Parkin (113); Scott (134), pp. 99–102, and (133), Pt. 2, pp. 427–429; Thomas (173, 174, 175, 176); Wieland (189), 2, 228 et seq., (191).
[2] Sinnott and Bailey(151, 152); see also Berry(17), chap. vi, for the probable physical conditions under which undoubted Angiosperms first appeared in North America.
[3] Compton(40); Eames(47); Hallier(63); Sinnott and Bailey(151); Seward(142); Worsdell(196).
[4] Adkinson(1); Bailey(12,13); Chrysler(36); Eames(47); Hallier(63); Jeffrey(90, 91,92); Jeffrey and Torrey(93,94); Lindinger(106); Sargant(130); Sinnott and Bailey(154); Whitaker(186). See also list of references to anatomical work bearing upon this point given later in the paper.

(5) The form of their leaves[1].

(6) The floral structure of Primitive Angiosperms, whether relatively simple or complex, or whether both conditions were represented; the presence or absence of petals[2]; and the mono- or diclinous organisation of the flower[3][4].

(7) The type of fruit they possessed[s].

(8) The number of cotyledons in their embryos[5]; and

(9) The type of their seedling anatomy[6].

These questions cannot be answered by reference to direct and positive evidence. It is not possible to say of any Angiosperm, living or fossil, "This is, or represents, a Primitive Angiosperm." The problems must be attacked indirectly by an impartial consideration of evidence drawn from a consensus of facts; and, in spite of much accumulated evidence, the question of the origin and nature of Primitive Angiosperms is still no more than a matter for speculation.

The question of the habit of Primitive Angiosperms is one which

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[1] Sinnott and Bailey (152).

[2] Arber and Parkin (8, 9); Brouwer (20); Campbell (31); Parkin (113); Senn (135); Wernham (185); see also Moss (112), for a review of Modern Systems of Classification, in which are discussed the views of various authors concerning primitive floral states. Papers by Pilger (116), and Vuillemin (182) may be briefly mentioned here, being of interest in reference to primitive types of whole reproductive axes; according to Pilger, the panicled inflorescence is primitive, and the single-flowered axis derived, while Vuillemin believes that the "Amphigonelle," or catkin-like reproductive apparatus, of the Juglandales, Salicales, Cupuliferae and other orders, is the lowest type amongst Dicotyledons.

[3] The hypothetical "Hemiangiosperm" flower of Arber and Parkin (8, 9, 113) is monoclinous; and in the Fossil Cycadophyta so often referred to in connection with the ancestry of Angiosperms, there is evidence that monocliny was the rule amongst the later, more specialised, members of the group (Scott (134), p. 85; Seward (137), 3, 379, 380, 456–459; Wieland (189), 1, 139 et seq.). Of the older types, *Williamsoniella coronata* and *Wielandiella* were monoclinous (Scott (134), pp. 96, 97), but the *Williamsonia* group as a whole are generally considered—though not proved—to have been diclinous. It is interesting to note, in this connection, that many families of woody Angiosperms represented amongst the earlier fossil-types of the group have diclinous organisation. (See later in the paper.)

[4] Sinnott and Bailey (153).

[5] Arber (3), chap. vii; see also discussions and references given by Holden and Daniels (83).

[6] For researches and discussions relating to type of seedling anatomy, transition phenomena and their phylogenetic significance, see Arber (2); Compton (39, 40); Davey (43); Hill and de Fraine (75, 76); Holden and Bexon (80); Holden and Chesters (81); Holden and Clarke (82); Lee (101, 102); Sargant (129, 130); Sinnott (148); Tansley and Thomas (165, 166); Thomas (168, 169, 170, 171, 172). (See other references given under the section on Seedling Anatomy; and also a report of a discussion on the Vascular Anatomy of Seedlings, at York, 1906, in the *New Phytologist*, 5, 1906, 182.

has received much attention, particularly from American botanists. As a result of their studies, chiefly anatomical[1], these workers have concluded that the arborescent habit is primitive for the group, and that the herbaceous habit is derived[2].

This conclusion is opposed to the purely theoretical views expressed, for example, by Campbell, by Coulter and Chamberlain, and by Coulter, Barnes and Cowles.

An evolutionary scheme given by Campbell indicates the suggested derivation of the Angiosperms from eusporangiate heterosporous Filicales ((31), p. 157). This author also remarks on the number of fossil members of the "Amentaceae," and points out that these may have been preceded by herbaceous forms of which there are no traces ((31), p. 229). Coulter and Chamberlain suggest the origin of Monocotyledons from an *Isoëtes*-like ancestor, and that of Dicotyledons from a *Selaginella*-like ancestor, on the ground of similarity of the embryos ((42), p. 287). As an alternative, they suggest a similar view to that held by Campbell. Coulter, Barnes and Cowles indicate that "trees are a recent development" ((41), p. 738), an adaptation to ecological conditions. These views imply, to a greater or less extent, the primitiveness of herbaceous forms.

It is proposed, in the present communication, to review the available evidence concerning the habit of Primitive Angiosperms.

II. Suggestions from the history of other phyla

Comparisons with regard to habit have been drawn between Angiosperms and other groups of which we know a part, at least, of the history from a study of fossil types (cf. Bailey(12), p. 235; Eames(47), p. 215; Sinnott and Bailey(151), pp. 549–550).

Before embarking upon these comparisons, however, it will be well to remember Professor Seward's dictum that "the study of the fossil record raises more problems than it solves" ((141), p. 597), and therefore to treat its evidence tentatively and cautiously.

The oldest members of the Equisetales at present known were arborescent, with well-marked cambial activity and considerable

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[1] Bailey(10, 11, 12, 13); Bailey and Sinnott(15); Eames(46); Flint(50); Hemenway(64); Hoar(77); Holden(84, 85); Sinnott(145); Sinnott and Bailey(150,152); Thompson(177); Torrey(181); Whitaker(187, 188). See also the list of references already given on p. 154, footnote 1; and a review of the earlier papers dealing with these anatomical studies, by Tansley(163).

[2] Eames and MacDaniels(47), chap. xi, pp. 245–248; Jeffrey(92), chaps. xiii, xxviii; Sinnott(149), chap. vi, pp. 101–104.

secondary growth; the geological record from Palaeozoic through Mesozoic to recent times, shows the gradual diminution in size of the individuals, the present-day Equiseta being herbaceous and typically without secondary growth, or with only a small amount of cambial activity at the nodes. The evidence, at first sight, seems to point in this instance to the derivation of the herbaceous from the arborescent type, by a process, as Jeffrey and Torrey suggest, of degeneration, manifested in the loss of cambial activity ((94), p. 246).

Further, the majority at least of the oldest known Lycopods were trees, and the present-day types are herbaceous. It has been suggested that the Triassic genus *Pleuromeia* may be a reduced intermediate form, linking the living herbaceous *Isoëtes* with the arborescent Carboniferous plants[1].

The evidence, then, in these two phyla, according to Eames, seems to favour the primitiveness of the woody, and the derivation of the herbaceous habit, the survival of the latter, as this author believes, being probably "due to an adjustment to modern conditions, involving the loss of secondary growth and the acquisition of a low or prostrate habit" ((47), p. 215).

In the case of the Lycopodiales, however, herbaceous and arborescent forms are known to have occurred side by side in the Carboniferous; *Miadesmia*, for example (16), was herbaceous, though it was obviously a specialised plant, and cannot be taken as representative of the Lycopod flora of the time. But various other small and apparently more normal non-woody plants have been referred to the genera *Lycopodites* and *Selaginellites* in the same group[2]; and since these herbaceous forms were contemporaneous with the arborescent Lycopods, it is impossible to say from any direct evidence which represents the more primitive condition for the group. In any case, as Halle has pointed out (61), the modern herbaceous Lycopods are more likely to be the direct descendants of the former, than to be degeneration products of the latter types.

There may, moreover, have been more of the herbaceous forms than are known, for woody plants are much more likely to be preserved as fossils than delicate herbaceous plants; so that the overwhelming majority of woody plants in the geological record of the

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[1] Seward (137), **2**, 72; see, however, Scott ((133), Pt. 2, p. 403), who remarks on the difficulty in accepting this suggestion, if, as is stated, the sporangia occurred on the underside of the sporophylls in *Pleuromeia*.

[2] Seward (137), **2**, 73–88. Note also that *Lepidodendron Harcourtii* is not yet known with secondary thickening; it may, however, be merely a non-thickened portion of a larger form (Scott (133), Pt. 1, p. 124).

Equisetales and Lycopodiales does not mean, necessarily, that non-woody forms were few in number in the early history of these groups.

It is debatable to what extent a comparison between the Equisetales and the Lycopodiales on the one hand and the Angiosperms on the other, is valid in the absence of sure evidence concerning the actual origins of the groups under consideration, and the physiological conditions under which they developed. The beginning of the phytological record shows the arborescent types of the Equisetales and Lycopodiales well established and highly developed. Their origin and ancestry are not known, and there is nothing to indicate the habit of the first members of these two phyla, or that of their immediate predecessors[1]. A belief in the algal ancestry of vascular plants is, however, general[2], and in view of the typically non-vascular nature of the Algae, it seems reasonable to suppose that, if the evolu-

[1] It is questionable how far the early Devonian "herbaceous" Psilophytales may be considered as the predecessors of any one group. They certainly show a simple organisation, and are so far synthetic in character, that the members of the Rhyniaceae have been variously referred to the Pteridophyta (Kidston and Lang(95), Pt. 1, p. 779; Scott(134), p. 191), and to the Thallophyta (Arber(7), p. 72). Comparisons have also been made between the Rhyniaceae and the Bryophyta (see Campbell (32), pp. 7, 8; and cf. Halle's *Sporogonites* (62), with Kidston and Lang's *Hornea Lignieri* (95), Pt. 2, pp. 611–616, plates 4–10); while Bugnon(30) proposes an entirely new group, "Thalloxylophyta," for the reception of undifferentiated types with a partly developed vascular system, standing in an ancestral relationship to the Bryophyta and Pteridophyta—or, at any rate, "acting as synthetic links" between the two groups (Bower(25), p. 9). At the same time, as Scott points out, it is not certain whether the simplicity of the Rhyniaceae is really an index of primitiveness, for its peat habitat was a specialised one, and the members of the family may represent the reduction products of some algal stock; moreover, the allied genus *Asteroxylon*, also from the Rhynie Chert-beds, had a much more advanced organisation, similar to that of a Lycopod and showing resemblances to the Psilotaceae, and to the Ferns also, if the assignation of reproductive structures is correct (Scott(134), pp. 191–195).

[2] Although the algal ancestry of vascular plants is generally conceded, there is considerable diversity of opinion concerning the *manner* of their evolution. According to some writers, vascular land plants evolved from simple forms on the land itself, producing the organisation suited to land conditions (Bower(24), p. 3; Fritsch(52), (53), p. 186; Lignier(105); Potonié(117)). Church(37), on the other hand, without reference to fossil evidence, holds that land plants arose from already highly organised transmigrant Algae, which had evolved from the free-swimming organisms ("Plankton") of a universal ocean, through the "Phytobenthon" stage of *rooted* plants, which succeeded to the Plankton stage as the sea-bottom began to rise. These rooted plants reached a considerable degree of organisation, so that, as the land emerged from the sea, it bore an already highly differentiated flora. Two objections to Church's contentions may be pointed out: a geological objection to the postulation of a "universal ocean"; and a biological objection to the possibility of highly developed plants adapting themselves to new, land, conditions.

Diversity of opinion also centres around the question of the mono- or

tion of land plants from simple types took place actually on land,
the first *vascular* land plants were at least not arborescent[1]; and in
this connection may be mentioned the opinion of Dr Scott, expressed
in his Presidential Address to the Linnean Society in 1909, that
cambial growth was at first most likely absent in the history of
vascular plants[2]. How far the Carboniferous Equisetales and the
Devonian and Carboniferous Lycopodiales were removed from the

polyphyletic origin of vascular plants. Halle ((62), p. 39) upholds the view of
their monophyletic origin from an ancestral group of vascular plants. Kidston
and Lang, while generally in agreement with Halle, think that the evidence as
to the origin of vascular plants is insufficient to allow of definite conclusions
((95), Pt. 3, p. 673; and Pt. 4, p. 843); these authors also suggest "the con-
vergence of Pteridophyta and Bryophyta backwards towards an Algal stock"
((95), Pt. 3, p. 675), a view approaching that of Lignier(103, 104), who referred
Pteridophyta and Bryophyta to an ancestral terrestrial group, the "Pro-
hepatics."

Church is emphatically in favour of the polyphyletic origin of vascular
plants, for he holds that all the main lines of the land flora were already
differentiated in the benthic stage, having had independent origins even as far
back as the unicellular (plankton) phase ((37), p. 41). Seward, in his Hooker
Lecture of 1922 ((130), pp. 237, 238), made a suggestion of polyphyletic origins
even more extreme than that proposed by Church. In referring to the difference
in type between Palaeozoic and Mesozoic Ferns, he suggested that trans-
migration may have been a recurrent, instead of a single, process. So that "it
is conceivable that plant-life viewed as a whole may best be represented by
separate and independent lines of evolution, or disconnected chains which
were never united, each being initiated by some revolution in the organised
world." Arber ((7), pp. 72–87), following in general the ideas of Potonié(117,
118, 119), also believed in the separate origin of the four main Pteridophytic lines
(Sphenopsida, Lycopsida, Pteropsida and Psilotales) from algal stocks;
interesting in comparison with Seward's suggestion, quoted above, is Arber's
view that the Psilotales evolved from the Algae much later than the other
groups "possibly in Mesozoic times or even later" ((7), p. 87). Scott ((134),
p. 202) concedes that the theory of polyphyletic origins of the main groups of
vascular plants "Lycopsida, Articulatae (= Sphenopsida), Ferns, and perhaps
the seed plants, is evidently quite tenable," though, in the present state of our
knowledge, "we cannot be certain that there may not have been a common
initial group of vascular plants, from which all the later lines diverged." He
concludes (pp. 204, 205) that the "question of the single or multiple origin of
the races of vascular plants must still be left open," because it is impossible to
determine whether the various similarities of structure and reproduction in the
main groups are due to affinity, or to "a like response to like conditions."
(See also Scott(132).)

[1] Cf. one of the letters of the late Professor H. H. W. Pearson to Professor
Seward, in which he stated his belief that "the first vascular plants must have
been herbaceous" (Seward(138), p. v).

[2] Scott(131), pp. 9 and 10: "It is an interesting question whether there was
ever a time without it" (i.e. secondary thickening). "Was the power of cam-
bial growth at some period or other, however remote, a new acquisition, or is it
as old as the vascular tissues themselves?...Widely spread as it was, the
evidence on the whole points to cambial growth having been a secondary
acquisition in the history of the race as in that of the individual plant....The
argument rests on the relatively great development of the *primary* vascular
tissues in many Palaeozoic plants, on the frequent sharp distinction between

first vascular plants, it is impossible to say; but it is conceivable that when vascular plants first evolved, the inherent vigour of the new group or groups led not only to rapid increase in the *number* of individuals, but also to a rapid increase in the *size* of the individuals, along one or more lines of development. The group or groups as a whole, and the various lines within the groups might, therefore, comparatively soon be represented by a large number of woody plants. In course of time, it may be supposed, a zenith of development was reached; subsequently, those members of any line which had attained great complexity and had thereby lost their plasticity, were unable to adapt themselves to any change of ecological conditions which might come upon them, and they, in consequence, died out. Other arborescent types, more adaptable, may have given rise to less woody types by reduction[1]; and thus the group slowly declined, coming to be represented only by the originally smaller and less complicated forms, and by reduced forms, the descendants of arborescent types[2] (Diagram 1).
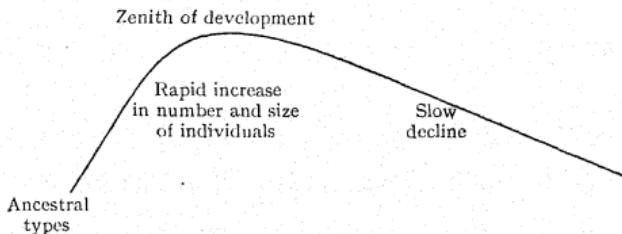
Diagram 1. The course of evolution of plant groups (e.g. Equisetales or Lycopodiales), according to the proposition outlined above. The Lower Coal-Measure Age probably marks the "zenith of development" of the Equisetales; that of the Lycopodiales was perhaps a little later.

primary and secondary formations, and on the late appearance of the latter in individual development." (See, however, the proposition advanced by Church, to which reference is made on p. 160.)

[1] Cf. Tansley ((162), p. 131), who states that there is "a great primary tendency to increase in bulk and complexity", and that subsequently competition leads to limitation, or a considerable reduction "in size and complexity; see also Eames (47), p. 215. Jeffrey and Torrey ((94), p. 246) refer to the Vascular Cryptogams as being represented in the living flora by "degenerate" herbs, cambial activity having ceased.

[2] Amongst animal phyla, the Reptilia as a whole, and also the Cephalopoda, show a notable parallelism with this scheme in their rapid development and comparatively slow decline. The same scheme also applies to the number, at least, of types and individuals in the Cycadophyta and Ginkgoales amongst other plant phyla (cf. Wieland (190), p. 404, and Diagram 2, p. 401).

It is evident, then, from the foregoing considerations, that ultimate primitiveness of the arborescent habit cannot safely be assumed for the Equisetales and Lycopodiales; and, in such case, a comparison of the Angiosperms with them in this respect is unlikely to produce data of any value.

It is necessary, however, to keep in mind Dr Church's suggestions, made independently of fossil evidence, that evolution of the various plant phyla may have taken place in the sea itself (see footnote 2, p. 157). According to this view, certain members of the marine "phytobenthon" giving rise to the land flora may have already possessed the arborescent habit, as in the recent genus *Lessonia*, or a shrubby habit, as in *Cystoseira* and *Sargassum* ((37), p. 24); in such Laminarian and Fucoid types, with their secondary growth from a meristematic tissue, "the essential features of a modern woody stem are immediately foreshadowed" ((37), p. 37). Further, "It is to the more massive, more resistant, self-supporting perennial stocks of marine phytobenthon, with massive crampon-attachment, large and active photosynthetic area, that one must look for the greater possibility of somatic adaptation to the new necessities of the problem; and so far, it will be among the higher Fucoids (*Sargassum*, *Turbinaria*) and Laminarians that analogies may be sought for the factors making for success in the first land-types of true Land-Flora" ((37), pp. 36, 37).

Church emphasises the fact that land plants cannot have "been evolved from Laminarians, but the latter may present a clue to the evolution of the mechanism" of secondary growth ((37), p. 83, footnote 1); and in this connection, it is interesting to note that Scott, while on the whole in favour of the secondary acquisition of cambial growth in land plants, admits the possibility of its having existed even amongst the earliest types, an admission to which he is led by the occurrence of secondary growth in present-day sea-weeds ((131), p. 10). It should be remembered here, that the fossil *Nematophyton* (= *Nematophycus*), referred to the Algae and compared with the gigantic marine sea-weeds of the present day, occurred in the Rhynie peat-beds with *Rhynia* and other members of the Psilophytales ((95), Pt. 5, p. 882); the association of this plant "with vascular land-plants in an inland locality suggests an unexpected degree of adaptability in the higher Algae of those days," as Scott points out ((134), p. 197). Church does not accept *Nematophyton* as a Laminarian (37), p. 49), but if, as seems likely, it was truly an Alga, it may have been a Chlorophycean type; and if so, it may provide an even

better clue to the development of terrestrial plants than the Laminarians themselves.

According to these suggestions, therefore, some at least, of the first true land plants may have been arborescent, with secondary growth; and the main Angiospermous line itself may have included woody types at its initiation, although in Angiosperms, "no direct evidence of the older epochs remains" ((87), p. 84).

Turning to other plant groups in passing, it is interesting to note that the Gymnosperms (including Pteridosperms), well-developed in Carboniferous and even in Devonian times, were, and still are, characteristically woody with well-marked secondary growth. This group, like the Equisetales and Lycopodiales, at first sight appears to support the idea of the primitiveness of the arborescent habit and of secondary growth, these characters having in the main persisted[1], particularly in the Coniferales—which are, of course, the successful Gymnosperms of the present day—without giving rise to any herbaceous types (see Sinnott and Bailey(151), p. 562). But here, again, the pre-Devonian history of the group is not known; and even if the Pteridosperms are regarded as representing primitive Gymnosperms, they are known only as contemporaneous with more highly developed members of the group, with which they possessed in common the power of secondary growth.

The Ferns, on the other hand, are known from Upper Devonian times onwards as a group in which cambial activity producing secondary growth never became established (Scott(131), p. 9), though it appears in various species of the recent genus *Botrychium*, in *Botrychioxylon* and *Metaclepsydropsis* amongst Palaeozoic ferns, and in *Osmundites Kidstoni* of Mesozoic times. It is significant that the later and more advanced ferns do not show secondary growth, although some of them (members of the Cyatheaceae), like some of the Palaeozoic types (Psaronieae), have assumed tree-like proportions without it (Bower(27), p. 294)[2]. It rather appears that a *capacity* for secondary growth was present in the early ferns, but that cambial activity was soon abandoned, in contrast with its retention in the Gymnosperms. But still there is no indication, from fossil evidence, that the ancestry of the Filicales was arborescent.

The Gymnosperms and Filicales, then, are no more productive of

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[1] Exceptions occur in the case of small Cycad types and members of the Gnetales; these however show, particularly in the latter case, adaptations to extremely specialised conditions.

[2] Cf. the Palms, amongst the typically herbaceous Monocotyledons.

decisive evidence, either one way or the other, than the two phyla at first discussed.

III. EVIDENCE FROM THE FOSSIL RECORD OF THE ANGIOSPERMS, AND PHYLOGENETIC CONSIDERATIONS

Although it appears doubtful whether the tree habit is primitive for vascular plants as a whole, the possibility of its primitiveness for the Angiosperms themselves is not precluded. Attention must therefore be turned to the fossil record of the Angiosperms, and to phylogenetic considerations.

Until recently, knowledge of the fossil record of the Angiosperms has indicated that they appeared suddenly in Lower Cretaceous times, and that by the Upper Cretaceous, many Angiosperms representative of Dicotyledons as a whole, together with some Monocotyledons, were in existence[1].

Newer work, however, is pushing the Angiosperm record further back. Simple ovate leaves (*Phyllites*) have been recorded by Professor Seward from the Stonesfield Slate of Jurassic age ((136), p. 152, Pl. XI); their appearance certainly suggests Dicotyledonous affinities, but it is not possible as yet to refer them more definitely to any systematic position.

Dr Hamshaw Thomas has recently described some undoubtedly "Angiospermous" fruits with enclosed seeds, and some stamens, from the Inferior Oolite (173, 174, 176); these are therefore of a greater age than *Phyllites*. The fruits are referred to the new genera *Gristhorpia* and *Caytonia*, and the stamens to the old genus *Antholithus*, while the new group "Caytoniales" is proposed for their reception; it is further suggested that the leaves long known as *Sagenopteris* may belong to these plants[2].

The Caytoniales are thus the oldest "Angiospermous" group so far recorded, for Hoskins' "stem," *Angiospermophyton*, of Palaeozoic age (86), cannot be accepted as an Angiospermous type[3].

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[1] Scott(134), pp. 42–56. See types given by Berry(17); Knowlton(96), pp. 142–170; Stopes(160); Stopes and Fujii(161). Note also Guppy's suggestion, in reference to Angiosperm evolution, that there was an "era of origination" and an "era of differentiation" ((59), pp. 161, 471); since Angiosperms were well differentiated by the Upper Cretaceous, the period of origination must have been considerably earlier. (Cf. Wieland's suggestions(190), p. 401, Diagram 2; and (193).)

[2] Thomas(174), pp. 331–340. Note that Berry(18) recommends caution in accepting both the angiospermous nature of the Caytoniales, and also their relationship with *Sagenopteris*.

[3] See Seward(140) who believes this supposed monocotyledonous stem to be a medullosean petiole.

Nothing appears to be known as to the habit of these very old Angiosperms. The vast majority of types recorded from both the Lower and Upper Cretaceous rocks, however, are woody, e.g. *Woburnia porosa*[1], one of the oldest species, from the Lower Cretaceous (Lower Greensand) of Bedfordshire, and *Jugloxylon, Fagoxylon* and others[2], from the Upper Cretaceous of Japan; while herbaceous types, e.g. grasses and sedges, increase in number in the younger strata ((96), pp. 165, 172). Thus, on direct evidence alone, it would appear that the arborescent habit is the older in the Angiosperms. But, as is well realised, the imperfections of the fossil record render it incapable of supplying trustworthy data on such a point.

Many speculations as to the immediate ancestry of the Angiosperms, however, reveal a prevailing idea that they are related to woody types such as those of the Cycadophyte alliance[3]. Arber and Parkin, in 1907 and 1908, suggested a relationship between the Angiosperms and the Gnetales through Ranalean types, the whole alliance having arisen from a hypothetical Mesozoic group[4]; this group—the "Hemiangiospermae"—Arber and Parkin included amongst the Cycadophyta. Parkin, in 1923 (113), restated this theory before the Linnean Society, and has since (114) shown a similarity of stomatal structure in Ranalean, Gnetalean and Bennettitalean types, which, he contends, is significant from the standpoint of the phylogeny of the Angiosperms.

The extension of the Angiosperm record into Jurassic strata makes it difficult to regard any group of Mesozoic Cycadophyta as ancestral to the Angiosperms, though, as Wieland suggested and maintains, the Angiosperms and the known Cycadeoids may have come from a common stock, the two groups going far back geologically ((180, 191); cf. Scott (134), p. 102). But the later Cycadeoid flowers, at least, show a specialisation comparable with that of the

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[1] Stopes (160), p. 92, Pl. 7, fig. 7, and Pl. 8, fig. 8. *W. porosa* is a type recalling the structure of the tropical Dipterocarps.

[2] Stopes and Fujii (161), pp. 62, 64; Pl. 7, fig. 48, and Pl. 8, figs. 50–53. See also Berry (17) and Knowlton (96) for Cretaceous Angiosperms.

[3] Arber and Parkin (8, 9); Parkin (113); Wieland (189, 190, 191). See also Carpentier (33).

[4] This suggestion was made with reference to the reproductive structures, and it is noteworthy that the stamens, at least, of the hypothetical "Hemiangiosperm" flower agree very closely with those of the subsequently described *Williamsonia mexicana* of Wieland (cf. Scott (134), pp. 92, 93). Thompson (178), on anatomical grounds, suggested a relationship between the Angiosperms and the Gnetales, though he believed the Gymnospermous affinities of the Gnetales to be with the Conifers rather than with the Cycadophyta. Thompson's later work, however, leads him to prefer a view of parallel evolution of the vascular structures of the Angiosperms and the Gnetales (179, 180).

more advanced Angiospermous flowers(192); the Gnetales, associated
by Arber and Parkin with the Angiosperms in a community of origin
from types of a Cycadophyte relationship, are specialised and
unusual forms, and nothing is definitely known concerning their
fossil history; the Ranales, so often referred to as a basal type amongst
Angiosperms, show a wide range of habit, including trees, shrubs
and herbs, the latter having probably arisen in response to special,
geophytic conditions. Such considerations increase the difficulty of
determining what may have been the prevailing habit of the ancestral
stock of Angiosperms.

Dr Hamshaw Thomas's researches on the Caytoniales have led
him farther back than Mesozoic times for the origin of the Angio-
sperms. In 1921, he pointed out that the Caytoniales may be a link
between Pteridosperms and modern Angiosperms(173), and in 1925,
he further suggested that *Glossopteris*, a probable Pteridosperm of
the Carboniferous flora[1], may perhaps represent the stock from
which both the Caytoniales and the modern Angiosperms were
derived ((174), pp. 353–354; (175)); this suggestion is based upon the
similarity of the *Sagenopteris* leaves, associated with members of the
Caytoniales, to those of the *Glossopteris* type. Little is definitely
known of the habit and structure of members of the *Glossopteris*
flora, though *Glossopteris* itself appears to have been low-growing,
with a creeping stem; and if this alliance does indeed include the
ancestral Angiosperm stock, enquiries from this source, also, are
somewhat barren so far as the habit of Primitive Angiosperms is
concerned[2].

It appears, therefore, that the fossil record of the Angiosperms

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[1] Cf. Walkom(183), who has described a seed, *Nummulospermum bowenense*,
associated with the leaves of *Glossopteris*, in the Permian of Queensland, thus
indicating the Pteridosperm nature of *Glossopteris*.

[2] At a meeting of the Linnean Society on January 21st, 1926(176), a more
detailed suggestion as to the immediate relationships of the Caytoniales was
made by Dr Hamshaw Thomas, namely, that though it is unlikely that they
"represent the direct ancestors of the flowering plants" (p. 22), there may have
existed, in Mesozoic times, a group of plants derived from Pteridosperms
which resembled the Caytoniales in the structure of their sporophylls, and the
Bennettitales in the strobilar arrangement of the sporophylls. "From such a
group, many of the modern flowering plants may have been derived" (pp. 24,
25). The seed structure of *Caytonia* indicates a relationship with the Bennetti-
tales, even though "somewhat distant"; this fact and the foregoing suggestion
again link the Bennettitales with Angiosperm ancestors, probably through a
common group of Pteridosperms. Berry(18), while cautious in accepting
Thomas's conclusions, points out that if they "are correct, then these Middle
Jurassic plants help bridge the gap between Gymnosperms and Angiosperms,
and introduce us to a type which combines fern-like foliage, and gymnospermous
seeds enclosed in angiospermous carpels."

themselves, and any speculations as to the origin of the group, do not help greatly towards a knowledge of its primitive habit.

IV. EVIDENCE FROM THE GEOGRAPHICAL DISTRIBUTION OF THE ANGIOSPERMS

Some evidence as to the relative antiquity of herbs and woody plants may be sought in a study of the present geographical distribution of the two types.

As Sinnott and Bailey have shown (151), the vegetation of the cooler regions of the globe is largely herbaceous, while that of the warmer areas is largely composed of woody plants; the climate of these warmer regions, according to Sinnott and Bailey, probably more nearly approaches that under which Angiosperms, as a group, first appeared[1].

Further, as these authors point out, land areas which have long been isolated must possess a flora which is very ancient, especially so far as the endemic forms are concerned; and it has been found that in the continental areas of the Southern Hemisphere, and in isolated islands, the most ancient members of the vegetation—that is, the species of endemic genera—are overwhelmingly woody; while the more recent members—the non-endemic species—are mainly herbaceous[2]. Sinnott and Bailey note that the *annual* herb, in particular, is generally lacking in isolated insular floras[3].

These facts, the authors conclude, indicate that the original Angiospermous flora of the world was for the most part, at least, composed of woody plants. The development of herbs, they suggest, was perhaps due in great measure to the progressive refrigeration of the climate during the course of the Tertiary era; and it seems to them not improbable that a large number of herbaceous types were developed on the mountains of the great land mass of what is now

[1] Sinnott and Bailey ((152), p. 17) state that it has generally been taken for granted that the Angiosperms came into being under a *tropical* environment; they claim, however, that the group must have had its origin "in a climate, which though doubtless very equable and devoid of extremes of temperature, was essentially a temperate one. Such a climate, so far as we are able to judge of conditions in the Mesozoic, could only obtain, as a general rule, in upland or mountainous regions." Since fossilisation in such regions would be rare, this suggestion is in accordance with the fact that comparatively few Mesozoic Angiosperms are known.

[2] Cf. Wallace, who remarks on the shrubby nature of endemic genera in the Hawaiian flora, these genera being represented elsewhere largely by herbs; he also notes the occurrence of "many strange arborescent Compositae, as in other oceanic islands" ((184), pp. 323–328).

[3] A criticism, by Mrs Arber, of this point is given later (p. 168).

the North Temperate Zone; that is to say, they were developed where refrigeration would be likely first to occur. Cooler conditions may have been effective in gradually and progressively stunting woody plants, until their aerial portions persisted only for a single growing season, and until, finally, the annual herb was produced ((151), pp. 597–599; see also Sinnott(147)).

If there is truth in Dr Hamshaw Thomas's suggestions as to the ancestry of Angiosperms amongst the *Glossopteris* alliance, the above considerations indicate a possible origin of herbs actually amongst the ancestral types of the modern group; for the dominant plants of the Permo-Carboniferous *Glossopteris* (or *Gangamopteris*) flora were apparently reduced in size as compared with the dominant plants of the immediately preceding Carboniferous flora, and the change in the type of flora coincided in time and distribution with widespread and severe glaciation and refrigeration affecting a large southern land area, known as Gondwana Land[1].

Herbs, with their short life cycle, are able to survive periods of cold underground or in the form of seeds, and having thus developed and become adapted to adverse conditions, they are "the most hardy and aggressive types of vegetation, and have consequently been able to invade successfully all regions of the globe" ((151), p. 596). In those families, of course, where trees and shrubs have been able to endure the cold, few or no herbs have been produced; this may have been the case in the Salicaceae, Betulaceae, Fagaceae, Rhamnaceae, Tiliaceae and other families.

Under adverse climatic conditions, herbaceous forms may also have been evolved in mountainous regions in the tropics, and in the Southern Hemisphere. Of considerable interest in this connection are Professor Small's speculations concerning the origin and development of the Compositae, a family composed chiefly of herbaceous species ((155), chap. xi); he gives a sketch of the transformation of a tropical arborescent Lobelioid type, *Siphocampylus*, into an Andean Composite type with all the essential characters of a *Senecio*, a genus including plants of very various habit, although, in this country, it is typically represented by herbs. Considering the Andes as a point of origin and dispersal of the Compositae, it is significant to note the number of species of the family recorded for this region by the explorer, Richard Spruce, and also his observations as to their distribution; for example, he says "from the mouth of the

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[1] See Knowlton ((96), pp. 103–109), for a summary of Permo-Carboniferous conditions, and of the flora of this period; also Seward(143).

Amazon to the cataracts of the Orinoco and the foot of the Andes, with the exception of a few scandent Vernoniae and Mikaniae, and of a few herbs on inundated beaches of the rivers, the species of Compositae that exist are weeds, common to many parts of tropical America, nor did I meet with more than one arborescent Composita (*Vernonia polycephala* DC.) in the whole of that immense area. But in ascending the Andes, from 1200 feet upwards, Compositae increase in number and variety at every step, and include many arborescent species" ((158), **2**, 288).

Many plants, particularly in the tropics, may have become herbaceous or semi-herbaceous through the assumption of the climbing habit, as in the Asclepiadaceae, Cucurbitaceae, Vitaceae and other families; and here again, Spruce's observations on the Andean Compositae are interesting, for amongst the shrubby and arborescent types of the higher altitudes, he also notes woody twiners, chiefly Senecionidae, and twiners of a more herbaceous type belonging to the Mikaniae ((158), p. 288).

With regard to tropical lowland herbs, many have, no doubt come down from the mountain areas—as, very probably, in the case of the Compositae of the Amazon; others have perhaps been evolved under tropical conditions as a result of alternating wet and dry seasons. Discontinuity in the amount of available moisture seems to have been the controlling factor in the production of herbs in desert and the drier regions generally; as Dr Willis notes, in his studies on geographical distribution, "So long as there is a reasonable amount of rainfall, not too much concentrated into one period of the year, the usual type of covering of the soil in countries that have not been disturbed by ice-periods, or by man, is forest"; and the general effect of climatic change, caused for example, by the development of a chain of mountains "transverse to the prevailing damp wind, is to encourage the growth upon the lee side of herbaceous and shrubby plants which can stand greater extremes of drought"((195), pp. 42, 43). While Sinnott and Bailey ((151), p. 595) are of the opinion that "the great mass of herbaceous vegetation" is of comparatively recent origin, they concede that it is "altogether probable that dicotyledonous herbs were developed in rare instances in the Cretaceous or very early Tertiary[1]," where they were exposed to local xerophytic conditions. Here, again, it may be pointed out that if herbs were

[1] Note that the Andes were developed in Cretaceous times, and Small ((155), chaps. xi, xii, xiv) suggests the origin and development of the Compositae in this area in the late Cretaceous or early Eocene.

developed under xerophytic conditions in Cretaceous or Eocene times, it is reasonable to suggest a still earlier inception of the herbaceous habit, in Angiosperms, namely, amongst the very first members of the group[1]—or, it may be, amongst their immediate ancestry in some differentiation period[2]—as a result of the arid, desert conditions of Triassic times, conditions which were possibly also effective in the reduction in size and woodiness of certain Equisetalean and Lycopodialean types.

Therefore, while the present geographical and climatic distribution of the Angiosperms may point, at first sight, to the comparatively recent development of many herbaceous types, there is no reason to believe that the earliest members of the group were exclusively woody. Opinions recently advanced by Mrs Arber(6), indeed, are definitely opposed to the view that any of them were woody. With regard to this question of geographical distribution, Mrs Arber quotes de Candolle's list of the most widely distributed flowering plants; each member of the list is a herb, and the indications are, therefore, that trees tend to be more restricted in distribution than herbs. Applying Willis's "Law of Age and Area," Mrs Arber suggests that this tendency broadly indicates the greater antiquity of herbs amongst the Angiosperms, though, as she admits, Willis himself(194) "has disclaimed the application of this theory to the problem of the relative age of trees and herbs" ((6), p. 73).

The lack of annual herbs in isolated insular floras, quoted by Sinnott and Bailey in support of their view of the derived nature of herbs (see p. 165), is explained by Mrs Arber as follows. A single unfavourable season may so hinder the setting of seed, that "a whole batch of immigrant annuals" may be exterminated at once. It is therefore more difficult for annuals to become established than for perennials, which are not dependent for continuance upon the seed of a single season. Further, Mrs Arber points out that isolated insular floras referred to in the literature are nearly always in the warmer and moister parts of the world, where the growth of woody plants is so favoured that they would tend to crowd out smaller plants such as annual herbs.

Finally, it must be borne in mind that speculations—such as

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[1] Note that Willis, in considering the factors which favour or inhibit the dispersal of species, comments on the possibility that herbaceous types may be very ancient, but restricted in distribution until new physical conditions favoured their dispersal ((195), p. 48).

[2] See p. 162, footnote 1; see also Wieland(190). Diagram 2, p. 401, and (193); Sinnott and Bailey(152), p. 17.

those quoted in the foregoing pages—concerning the climatic con-
ditions of previous ages and their possible effect on vegetation, do
not necessarily greatly contribute to a solution of the problem of
habit-evolution in the Angiosperms; for, as Professor Seward has
recently maintained, a correlation of present-day plant type and
climate may not be taken too definitely as an index to the correlation
of plant type and climate of other ages; in the course of time, plants
may have changed "in their susceptibility to external factors";
and "we are not entitled to attribute to extinct and recent alike the
same constitutional qualities" ((143), p. 214).

(*To be continued.*)

THE GEOGRAPHY OF THE GENUS *CORIARIA*

By R. D'O. GOOD, M.A., F.L.S.

(With 1 map in the text)

THE family Coriariaceae is a very isolated group of Dicotyledonous plants containing only the one genus *Coriaria* Niss. ex. L. (*Hetero-cladus* Turcz., *Heterophylleia* Turcz.). Its floral structure differs from that of any other family, and its systematic position and relationships have always been undecided. In De Candolle's *Prodromus* (1) it is treated as an anomalous family, placed after Ochnaceae, and this course is followed also by G. Don (2) and by Lindley (4). Endlicher (3) also considers it of doubtful position, but puts it at the end of Malpighiaceae, in which he is followed by Le Maôut and Decaisne (7). Bentham and Hooker (5) again describe it as anomalous, but place it after the Sapindales. Baillon (6) includes it as a series of his Rutaceae, but with the qualification that it probably represents a distinct order. In 1881 there appeared a revision of the genus by Maximowicz (8) which summarises our knowledge of the group up to the time of publication. It includes a lengthy discussion on the possible and probable affinities of the genus and family, from which the writer concludes that the closest relationships are with the Simarubaceae on the one hand and the Phytolaccaceae on the other. Engler and Prantl (10) place the family in the Sapindales as a sub-order of its own, Coriariineae, between Empetrineae and Limnanthineae, and this has been the treatment followed in the various editions of Engler's *Syllabus* (9). Wettstein (11) also recognised a similarity with the Empetraceae and sets the Coriariaceae between that family and the Cyrillaceae, all three being included in the order Celastrales. Hutchinson (12) makes of it a distinct order between Dilleniales and Pittosporales. In short, the Coriariaceae have almost always been recognised as anomalous, and there is no direct indication nor even consensus of opinion as to its position in a natural classification.

The genus *Coriaria* consists of woody plants ranging in size from semi-woody undershrubs to trees of considerable dimensions. The leaves are small, entire and pointed, and vary in outline from narrow elliptic or sub-linear to cordate. Their venation is simply palmate, conspicuous, but not peculiar. The rather inconspicuous greenish flowers are borne in racemes, and are unisexual or hermaphrodite, monoecious or dioecious or polygamous. Normally there is a 5-leaved

calyx, a 5-leaved corolla, 10 stamens and a superior ovary of 5–10 free carpels. In fruit the petals become fleshy and coloured, enclosing the 5–10 hard cocci. Each carpel has a single pendulous ovule with a thin endosperm and two integuments.

Species of *Coriaria* seem never to be deliberately cultivated, but the wild plants are put to some use by the natives of most of the countries in which they are found. Most of the species have deep purple or black "fruits" which provide a stain or an ink, and some can be used for tanning. All seem to be more or less poisonous, the cocci especially being occasionally fatal to both man and beast. On the other hand, the fleshy petals of certain species can safely be eaten or used in the manufacture of wine. Several crystalline glucosides have been isolated from the plants, and these are presumably the source of the poisonous properties. Some use is made of the timber of the larger forms (15, 21, 31).

The recognition and discrimination of species within the genus is a matter of extreme difficulty, partly because of the enormous range of continuous variation and the consequent lack of characters of absolute taxonomic value, partly because of the readiness with which hybridisation naturally occurs and partly because of the numerous ecological forms recognisable in the field (23, 24, 25, 28). This state of affairs makes it quite clear that an adequate systematic revision of the genus can only be carried out by one familiar with the plants in their native places and able to study them there, where characters not exhibited in herbarium material may become apparent. Therefore no attempt is made here to revise the genus, and its geography only is discussed. It is frequently necessary to refer by specific names to certain fairly definite forms within the genus, and in these cases the commonest or most widely known species-name is used without any inference or assumption that this name is the correct one according to the rules of nomenclature, or that the form for which it is used is unquestionably specifically distinct from others.

Despite these difficulties it is, fortunately, possible to divide the individuals of the genus into three groups or sections based on certain conspicuous and constant vegetative characters, visible in nearly all preserved material.

In the first group, A, the racemes are large, solitary and terminal, without bracts, and bear polygamous flowers. This group is a small one containing only what has always been considered a single species, *C. terminalis* Hems., and its variety or colour form *C. terminalis var. xanthocarpa* Rehd. et Wils.

In the second group, B, the racemes are short, generally clustered, lateral and axillary, always surrounded at the base by a ring of bud scales, and bear unisexual and/or hermaphrodite flowers. To this group belong the forms described under the specific names *C. myrtifolia* L., *C. tinctoria* Dulac, *C. hermaphrodita* Turra, *C. nepalensis* Wall., *C. japonica* A. Gr., *C. sinica* Max., *C. intermedia* Matsum., and *C. summicola* Hayata.

In the third group, C, the racemes are long, generally clustered, lateral and axillary, never surrounded at the base by bud scales but subtended by rounded leafy bracts, and bear hermaphrodite flowers.

To this group belong those forms described under the names *C. ruscifolia* L., *C. sarmentosa* Forst., *C. Tutu* Lindsay, *C. lurida* Kirk, *C. thymifolia* Humbl. et Bonpl., *C. angustissima* Hk. fil., *C. arborea* Lindsay, *C. microphylla* Poir., *C. phylicifolia* Humb. et Bonpl., *C. atropurpurea* Moç. et Sesse, *C. cuneifolia* Moç. et Sesse and *C. papuana* Warb.

Russow (13) has pointed out that the second and third groups can be distinguished by the following characters: in B the inflorescences develop on wood of the previous year and the primary medullary rays do not reach the pith, but are separated by strongly thickened interfascicular tissue like wood-prosenchyma: in C the inflorescences develop on branches of the current year and the primary medullary rays extend to the pith.

Several fossils have been described as Coriarias but, with two exceptions, they are simply remains of isolated leaves which may or may not belong to the genus. These latter can be dismissed here as too unreliable to warrant further notice. One of the exceptions is, however, of very great interest. It is a well-preserved fossil consisting of a complete spray some inches in length, having leaves, stems and a long terminal raceme, all organically attached. The long terminal raceme has already been mentioned as a characteristic of section A of the genus, that section containing only one species, *C. terminalis*, and there can be little doubt that the fossil represents that species or a closely allied one differing from it only in characters so small that they are not apparent in the fossil. It comes from the Armissan beds of Oligocene age, near Narbonne in south France, while the living *C. terminalis* is confined to the Himalayan and western Chinese mountains, and it was described as *C. longaeva* Saporta (26). It is interesting to note that to Saporta belongs the credit of first recognising that *C. terminalis* differed markedly from *C. nepalensis*, with which it had been confused, and that he obtained Hooker's con-

firmation of his view. The new species was not described, however, till many years later by Hemsley (37).

The other exceptional fossil is a carpel from the Pliocene of the Dutch-Prussian border. This has not been identified satisfactorily, but has been placed tentatively in the genus *Coriaria* by C. and E. M. Reid (27). Bearing in mind the extremely cautious and painstaking work of these investigators and their wide knowledge of present-day fruits and seeds, even this queried determination is of great interest and, at all events suggests, if it does not indicate directly, the presence of the genus, in Pliocene times, far to the north of its present range. It should be noted however that the fossil lacks the ridges so characteristic of *Coriaria* fruits.

GEOGRAPHY

The large mass of data, forming the basis from which the following geographical account of *Coriaria* is compiled, has been obtained by the personal examination of the collections in Herb. Mus. Brit. and Herb. Kew, and from lists of localities and rough determinations of the specimens of the genus in some twenty of the larger herbaria all over the world. My obligations to the institutions concerned are acknowledged in detail at the end of this paper.

From these sources the records of over a thousand herbarium specimens have been obtained and and their localities plotted on outline maps as accurately as possible. These maps were then compared with the records of the genus in Floras and other publications, and it was found that no important geographical records remain unsupported by one or more actual herbarium specimens. The record does not, of course, represent a thousand different collectings or localities because there is a considerable amount of duplication between the different herbaria, but the prominence of this duplication is significant because it indicates that a very great proportion of all the preserved material has been noted, and that in remaining herbaria the genus is likely to be represented only by such duplicated numbers. It is interesting to note in passing that there are specimens in the two great London herbaria from all the important localities of the genus.

The special importance of *Coriaria* from the geographical point of view lies in its unique degree of discontinuity. A considerable number of genera with distributions over two widely separated regions is known, and a few genera range over three such regions, but, so far as I am aware, *Coriaria* is the only genus occurring in four widely separated parts of the world (36). These parts are:

(a) The western Mediterranean;
(b) Continental and insular eastern Asia;
(c) Australasia, including parts of Polynesia: and
(d) Central America and western South America.

DETAILED DISTRIBUTION

Mediterranean. In the western Mediterranean the genus is found throughout the southern and eastern coastal parts of Spain, in the provinces of Seville, Granada, Murcia, Valencia, Aragon and Catalonia, and as far west along the Pyrenees as about the meridian of Greenwich. It is not found wild in Portugal. In south France it extends from the Hautes Pyrenees on the west to the Italian frontier on the east, its northern limits being reached, on the west, in the valley of the Lot and, in the centre, in the Department of Ardèche. Round the mouth of the Rhône it is rare but it is plentiful throughout the Departments of Var and Alpes Maritimes. Still following the coast it extends eastward in north Italy to include Liguria and western Emilia as far as long. 10° E. This point is its eastward Mediterranean limit. It is recorded from Trieste but not as a wild plant. Among the Mediterranean Islands it is found native on Majorca and Corsica, and as an introduced plant has been collected in Sicily. Along the North African coast it ranges from western Morocco, lat. 6° W., to the eastern edge of Algeria. As might be expected, the records from North Africa are fewer than those from Europe and the range shows larger gaps. In certain Floras the genus is vaguely reported from the Peloponnesus, apparently on the original testimony of Bory, but I have seen neither specimens nor other confirmation of this.

It will be seen that this part of the generic range is entirely confined to the western Mediterranean lands and, except perhaps in south-west France, is distinctly maritime. There is now only a single species, *C. myrtifolia* (Provençal Sumach), the type species of the genus, in this region. It is a plant chiefly of dry woods and rocky places and pastures, but is sometimes found near streams, and it occurs at all levels up to about 2500 ft. (19).

Asiatic. On the eastern Asiatic mainland the genus ranges from Kashmir to central China. Its southern limit passes along the Himalayan mountains to Assam and Burma, its extreme southern point being in the Shan States. From here the edge of its range turns north-east, to include Yunnan, and passes on to about long. 113° E. in central Hupeh. Thence it runs north to lat. 36° in Kansu.

The northern limit of its range runs from Kashmir along the north of the main mountain ranges to, roughly, long. 100° E. and lat. 30° N. in western Szechuan, whence it turns north-east to Kansu. The Asiatic mainland distribution thus consists of a narrow N.W.–S.E. western arm and a much broader eastern part with its main axis S.W.–N.E.—an outline commonly found among species and genera of this part of the world. The whole is fairly well covered with records, except where, as in Nipal and Bhutan, exploration has been particularly slight.

On the Asiatic islands the genus ranges from between the north latitudes 40° and 16°. In Japan it is found throughout the southern half of Yezo and southwards through Nippon as far as about long. 135° E. and lat. 34° N. There are two records from the Liu-Kiu Islands, both collected by Faurie, one from an island unlocalised and one from Nambu, the island group nearest Formosa. In Formosa the genus seems fairly widespread and is recorded from low levels and from the summits of the higher mountains. Lastly it is fairly widespread in the mountainous northern part of Luzon, the main island of the Philippines, but has apparently never been seen further south than lat. 16° N.

The plants of the Asiatic mainland have been grouped under three species, one of these being the well-marked *C. terminalis*, the only representative of genus-section A. It extends along the main mountain axis from Sikkim (and possibly Nipal) eastward as far as western Szechuan, in thickets between 6000 and 12,000 ft. The other two species are *C. nepalensis* and *C. sinica*, of which the typical forms are found in the Himalayas and in China respectively (28). The two are very alike and there is a good deal of confusion between them. The former seems to be found at levels between 3000 and 10,000 ft. while the latter is generally found below 3000 but sometimes as high as 4500 ft. It may be noticed as a passing point of interest that, despite its wide difference from all other species of the genus, *C. terminalis* was for many years confused with and identified under *C. nepalensis*. The last-named is closely related to the Mediterranean *C. myrtifolia*.

The Japanese plants have always been identified as an endemic species *C. japonica*. Formosan plants have been placed under two species, one, *C. intermedia*, including also the Philippine members of the genus, and the other *C. summicola*, being endemic and containing only the high altitude (8000 ft.) individuals. The plants of the Philippines are found chiefly from 4000 to 6000 ft. The plant from

Nambu has been identified as *C. intermedia*; the other Liu-Kiu specimen is undetermined.

The total Asiatic range of the genus may be summarised as follows. There is a large continental area comprising the Himalayas, parts of Assam and Burma, and much of China in which are found the single species of section A and what are generally taken to be two species of section B. The genus is also found in the central parts of Japan, on the Liu-Kiu Islands, in Formosa and in northern Luzon. Three species have been described from these insular regions, all of them belonging to section B.

Australasia. New Zealand is the great centre of the genus *Coriaria* in this part of the world, and over the whole of it, including Stewart Island, representatives are plentiful. It occurs also on Chatham Island, 500 miles east of New Zealand, and on the Kermadecs about 500 miles N.N.E. Much farther to the north the genus is found, widely scattered, in Samoa, Fiji, the New Hebrides and in Papua. From all these the records are very scanty and the localities rare.

There is very great difficulty in the identification and separation of species in this Australasian region. From New Zealand a large number of species have been described but hardly any two systematists agree upon their arrangement and value. The genus here exhibits a wide range of habit from the arboreal types, which form forests on parts of the western coasts, to low undershrubs on the higher alpine zones, and added to this, natural hybrids are common. A considerable amount has been written about the New Zealand Coriarias and some of the more important references are given in the bibliography at the end of this paper. These must be referred to for further information but it may be stated here that the commonest forms are those described under the names *C. arborea*, *C. lurida*, *C. ruscifolia*, *C. thymifolia* and *C. angustissima* (15, 20, 23, 24, 25).

Fortunately outside New Zealand proper the confusion is less. On Stewart Island, as might be expected, the plants closely resemble those of New Zealand and have usually been given the names *C. ruscifolia*, *C. thymifolia* and *C. angustissima*. On Chatham Island only one form is found, that known as *C. ruscifolia*. The same is true of the Kermadecs, of Fiji, of Samoa and of the New Hebrides (Banks Island). In the last-named the plant grows in the crater of an extinct volcano at an altitude of 3000 ft. In Papua, on the other hand, the plants have been described as a closely allied but distinct species, *C. papuana*.

All the plants from the Australasian region belong to section C— a section not represented in the northern hemisphere, except in Central America.

American. In the new world *Coriaria* is found northward from about lat. 45° S., along the western or andine part of the continent as far as the uplands of North Mexico on the Tropic of Cancer. There is a slight extension eastward along the mountains of northern Venezuela. The distribution over this whole wide area is not perfectly even but there is only one marked gap and the whole new world range of the genus can be treated as one.

The plants themselves, however, fall into two groups. In Chile, from the Tropic of Capricorn southward, is found a form of the genus which is generally considered as being identical with *C. ruscifolia* of New Zealand and other parts of Australasia. It is found from sea level to as high as 6000 ft. in humid thickets and is entirely restricted to Chile except for one record just over the Argentine border at lat. 43° S. (18). Between the Tropic of Capricorn and south Peru there are some hundreds of miles where *Coriaria* seems not to occur. Northward from about lat. 15° S. it is again common, this time in the alpine zones, especially in the inter-andine and east-andine tracts, at altitudes of from 4000–11,000 ft. in South America and from 4000–8000 ft. in Central America. There are two minor gaps in this latter region, the genus being unrepresented from Salvador, Honduras and Panama, though this apparent absence may be due to insufficient collecting at the higher levels. All the plants found between lat. 15° S. and lat. 23° N. are generally considered to belong to another New Zealand form, *C. thymifolia*, but before this similarity was fully realised the species *C. microphylla*, *C. atropurpurea*, *C. phylicifolia* and *C. cuneifolia* were described, mostly on very insecure bases.

The new world distribution of *Coriaria* consists, therefore, of the almost contiguous areas of two taxonomic forms, together stretching along the mountains from lat. 45° S. to lat. 23° N. Whatever the real value of these forms they are apparently identical with two of the Australasian forms, and, of course, represent the same section C. It may be mentioned here that certain systematists consider that all the southern hemisphere plants belong to a single, highly polymorphic species.

GEOGRAPHICAL SUMMARY (FIG. I)

Coriaria is found throughout the coastal regions of the western Mediterranean: in eastern Asia, from the western Himalayas to central China and in Japan, Formosa, Luzon and the Liu-Kiu Islands:
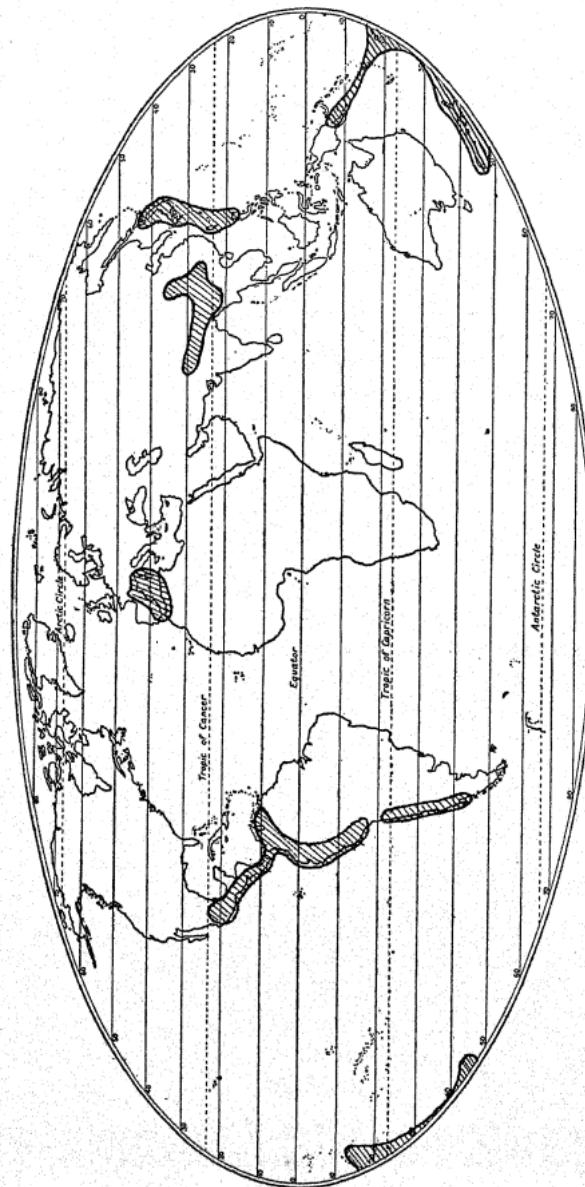
Map showing the present distribution of the Genus *Coriaria*

throughout New Zealand, including Stewart Island, and on Chatham Island, the Kermadecs, Fiji, Samoa, New Hebrides and Papua: and throughout Pacific America from south Chile to northern Mexico. The Australasian and American species appear to be identical: the species of the northern and southern hemispheres belong to different sections of the genus: the one monotypic section is confined to the Himalayan-western Chinese mountains.

<center>DISCUSSION</center>

The following pages are devoted entirely to discussing the particularly outstanding feature in the geography of *Coriaria*, its unparalleled discontinuity, especially in relation to the history of the genus and to the geography of the past. This feature of discontinuity is not infrequent among flowering plants, and is found in a small but appreciable percentage of all the genera (36). The great majority of these exhibit it only in its simplest form, the division of the general area into two widely separated parts. Some others are so distributed as to have three separated areas, but very few, perhaps none except *Coriaria*, have a range over four quite distinct parts of the world.

<center>*General remarks on discontinuity in the Angiosperms*</center>

The genera of flowering plants show such an extraordinary diversity in the details of their distribution that it seems, at first glance, almost impossible to divide them up according to their geography. Any detailed classification in this way is, indeed, impracticable, but if sufficiently broad features are taken it becomes possible to recognise a few principal well-marked types. Discontinuous genera form one such type, wide continuous genera form another, and endemic genera a third, the last being further divisible into those which are monotypic and those which are not, as well as according to the degree of endemism. Beyond this the matter becomes increasingly difficult, simply because there are nearly as many kinds of range as there are genera and hardly any two or more occupy exactly similar areas. Even for the primary classification just mentioned it is necessary arbitrarily to define the use of the term discontinuous, as it is at best relative and very few genera of any geographical size are absolutely continuous. As in a previous paper (36) the term here refers to separations of different parts of the genus by land or sea of continental or oceanic dimensions.

The difficulty of classifying Angiosperm genera according to their geography, owing to their great diversity in this respect, is significant.

Every state of distribution from endemism to pandemism, and from continuity to complete discontinuity, is represented. Such a series as this showing almost every intermediate stage between two or more extremes is a common biological phenomenon and is usually interpreted as evidencing a gradual process of change from one extreme to another in one or both directions. That such an explanation is applicable to the geography of Angiosperms seems probable from the following considerations.

Every newly evolved genus (the genus being the unit with which this paper is particularly concerned) must for a varying time after its origin consist of but a single species with a continuous and comparatively small range. As new species are produced and dispersal continues both the taxonomic and geographic size of the genus will increase. Gradually the speed of this increase will tend to lessen, not only because a time comes when new species can no longer be covered by the diagnosis of the genus and hence represent some other, but also because certain other and older species become extinct. Ultimately the stage will be reached at which the loss outweighs the gain, and the genus will actually decrease in size. Such a decrease, assisted by similar changes of climate and other less important factors, will lead almost inevitably to the development of discontinuity in distribution. Finally, if and when the genus loses all but one of its species and becomes extinct in all but one of its areas, it will have reached once more the state at which it commenced—that of a monotypic endemic.

The study of Angiosperm geography in general is certainly assisted by this conception, but it is obviously absurd to suppose that all genera pass through the whole cycle of chance. A great many factors will tend to disturb the suggested sequence of events. Increase in size, in age and in species by no means necessarily go hand in hand and, indeed, only rarely appear to do so. Similarity in range is not necessarily indicative of similarity in age. There is no reason to assume that the rate of species production is in any way constant for any considerable number or groups of genera. The factors influencing extinction may react far more severely upon some genera than on others, while other factors may prevent any increase either in size or area. More important still, the different stages in the cycle may have widely different time values. The monotypic endemic stage may be short or long, the pandemic stage may be brief or may persist almost unchanged for a long period. Absence of secular climatic change and other dangerous factors may delay or eliminate

entirely the discontinuous phase. A moment's consideration will suffice to call many other similar points to mind.

Despite these modifications the hypothesis of a geographical cycle is of great value on two counts. First it supports the view that endemic genera are either "new" or "old", either original or relic, but also indicates that since all genera are small in youth but not necessarily so in age, the majority of endemic genera are new or young genera. Secondly it shows that the three most conspicuous categories of distribution, the endemic, the pandemic-continuous and the discontinuous, represent three important successive stages in the complete geographical cycle which all genera *tend* to undergo in absence of disturbing factors during their history. Especially does it indicate that endemism represents in most cases a juvenile generic condition; that pandemic-continuity represents a mature or optimal generic condition, and that discontinuity represents a senile or diminishing generic condition. From the point of view of *Coriaria*, in particular, it affords definite reason for supposing that the discontinuity exhibited is indicative of great generic age.

The valuation of discontinuity as evidence of age requires modification in one respect, and to explain this it is necessary to anticipate the later discussion of theories of continental displacement. If the idea of continental displacement is supported it becomes clear that discontinuity may arise in two perfectly distinct ways, by the extinction of individuals in and disappearance of the genus from parts of a continuous area, or by the shifting and drifting of a region over which the genus is continuous. The theoretical importance of this is that while the first process naturally suggests considerable age, the second does not, since the discontinuity will date only from the initiation of drift, and this in turn may be ancient or recent according to the speed of movement. In the first, extinction is inevitably concerned, but not in the second. Hence, if displacement is postulated, discontinuity may result directly from any existing stage of distribution, even the endemic one, and may cause a complete short circuiting of the geographical cycle outlined above.

These considerations may be crystallised into the following working hypothesis of Angiosperm distribution. Every genus commences as an endemic monotype. Gradually, under the influence of time, dispersal and the production of new species, a varyingly wide but still continuous range is developed. Later, owing to the accumulated divergence of new species and the extinction of the older ones, the number of species in the genus tends to dwindle and the range to

become discontinuous. Finally, at its extreme expression, the genus is once more reduced to the condition of an endemic monotype, by the extinction of all but one species and the disappearance of all but one area. This complete cycle may be modified in various ways and by various means, but three phases in generic geography will normally appear: the monotypic continuous or juvenile stage; the polytypic continuous or mature stage; and the discontinuous or senile stage. Modifications are brought about chiefly by factors of secular climatic change. In particular the development of discontinuity by continental displacement may completely alter or shorten the geographical cycle.

This hypothesis of a geographical cycle leads to the immediately important conclusion that discontinuity of range generally indicates a stage towards senility in genera and the resulting inference that such genera are of considerable age. In the case of *Coriaria*, at least, it will be seen that this contention is fully borne out by all the additional lines of evidence.

The discontinuity of Coriaria *in the northern hemisphere*

Four main types of generic discontinuity can be seen in the more temperate parts of the northern hemisphere. Most of the genera concerned are confined to this region, but some extend southward into or even across the tropics, while a few, of which *Coriaria* is an example, are found also in the southern temperate.

The best known and most important of these types contains genera found only in Atlantic North America and in eastern Asia. Attention to this type of distribution was first called by Asa Gray, but it has been especially noticed much more recently because of the great increase in the numbers of this type resulting from the botanical exploration of the less-known Chinese mountain ranges. This is by far the largest of the four types, and the genera differ considerably in the extent of their Asiatic ranges. Some are found only in the mainland, some only in the islands (Japan, etc.) and others in both.

The second most noticeable type is that of the genera found only in North America (often the western part) and in Europe and/or western Asia. This is not a large group, but contains several genera familiar to European botanists.

The third type consists of genera found in Europe and/or western Asia and in eastern Asia. In all these is a marked gap towards the centre of the continental mass. This is the smallest of the groups and is of comparatively little but theoretical importance.

The fourth and last type is specially interesting because it combines the features of the other three. It is made up of genera found scattered more or less over the whole hemisphere, but with at least one marked discontinuity. This discontinuity is nearly always in the central parts of Eurasia, so that the great majority of genera are found in North America, Europe and/or western Asia and in eastern Asia.

The complementary nature of these four types seems to indicate clearly that the same ultimate factor has been the cause of all, the present differences between them being due to the interaction of this factor upon genera of varied age and geographical distribution. It appears, in fact, that the present types of discontinuity have been derived by the action of a single cause upon a number of pre-existing distributional types. There is a general agreement of opinion that this general factor was the great climatic change which commenced in the Tertiary and culminated in the great glaciations of the Pleistocene.

This explanation has been applied especially to the elucidation of the first of the above-mentioned types, the eastern American-eastern Asiatic discontinuity. It is supposed that, prior to the Pleistocene, these genera were distributed more or less completely longitudinally over the northern hemisphere. With the increasing cold the whole vegetation was forced to migrate southward, so as to keep pace with the moving climatic zones. In America no orographic or topographic barrier was presented to this southerly movement, and it is thought that on this continent the vegetation moved south as far as was essential, and retraced its steps when the ice retreated, being little destroyed or confused in the process. In Eurasia, however, circumstances were rather different. The effect of glaciation was progressively less from west to east, and while in Europe it was almost as severe as in North America, it was felt much less in eastern Asia. Moreover, there was and is an enormous mountain mass in that region calculated to provide an almost inexhaustible range of plant habitats and potential retreats. It is supposed that the general effect of the glaciation in Eurasia was to drive the European flora far to the south, but to leave the more easterly vegetation progressively less affected and moved. In Europe, however, there were orographical and topographical barriers in the path of the southern migration, with the result that many of the floral types concerned were exterminated in this area. In short, the terms of this theory suppose that the plants at present found only in eastern North America and in eastern Asia are some of those which, before the Pleistocene, had a very wide range over North America and Eurasia. What little

evidence the fossil record affords supports this view, especially since many of the plants are known as fossils in Europe and very many, if not all, the Angiosperm fossils of North America represent plants still existing there. There is also important evidence for the belief that parts of North America remained unglaciated, and that some of the pre-existing vegetation may have survived the Pleistocene without extensive migration.

Similarly, those plants at present found in North America, eastern Asia and in Europe and western Asia may be considered to represent types which, before the Pleistocene, also had a wide northern longitudinal range, but which by some fortunate circumstances escaped absolute extermination in western Eurasia and persist there to-day as relics of their former wider distribution.

The same basal factor of the Pleistocene glaciation can also be made to explain the other two types of discontinuity, the North American-European and the European-Eastern Asiatic, on the assumption that the former type represents plants with a pre-glacial range over North America and western Eurasia and the latter those with a pre-glacial wide Eurasian distribution. To this latter group, of course, belongs *Coriaria*.

This basal theory is quite satisfactory as far as it goes, but it does not explain satisfactorily the absence of all four types from central Asia where, in view of the comparatively small effect of glaciation, they should theoretically be found. An additional hypothesis is needed here, and the most usual and satisfactory is that this central Asiatic gap is due to secondary climatic changes which may have existed before the Pleistocene but which probably have developed since. At present this region is largely one of steppe and semi-deserts, but there is abundant historical and archaeological evidence that this is the result of increasing desiccation during recent geological time, especially and perhaps entirely since the Ice Ages, and that previously climatic conditions were quite different. Such changes as these are amply sufficient to account for a vast change in the vegetation of central Asia and an almost complete elimination of the more hygrophilous types.

It is appropriate to mention here the opinion held by some meteorologists and especially elaborated by Brooks (29) as to climatic conditions preceding the Pleistocene. This is that during the great part of the Tertiary the climate over the northern hemisphere at least was comparatively constant, with much more gradual latitudinal temperature gradient than at present and with entire

absence of Arctic conditions, and that the great glaciation came as a sudden and devastating change unparalleled during vast geological time previously. This supports the theory of discontinuity in the north described above, and is directly correlative with our knowledge of pre-glacial northern Angiosperm floras.

From this argument the present range of *Coriaria* in Europe and eastern Asia is taken to indicate that the genus had, through much of the Tertiary, a very wide and perhaps complete Eurasian distribution, and that the breaking of this distribution was caused by climatic changes associated with the glaciation of the Pleistocene.

But this view assumes that the genus has never been an inhabitant of North America, and such a view must be largely suppositional. It is, however, significant that no North American fossil Angiosperm has ever been identified as a *Coriaria*. This is, of course, merely negative evidence of questionable value, but it must be borne in mind that the identification of Angiosperm fossils involves a very careful and exhaustive comparison with living forms, and the absence of an American *Coriaria*-identification does indicate that no fossil strikingly and particularly resembling that genus has ever been found in North America. More than this cannot be said, and the genus may yet be found there in a living or fossil condition.

Another important point in connection with the view that *Coriaria* was widely distributed in Eurasia before the Pleistocene is the clear identification of the genus in European beds of Oligocene Age. This at once pushes its history far back into the Tertiary. Since, as has been shown above, there is no reason to assume that forced migration drove *Coriaria* into eastern Asia during comparatively recent times, it is justifiable to presume that its present discontinuity in Eurasia is the remnant of a former continuous range attained during the middle part of the Tertiary.

This palaeontological record is remarkable for another reason, namely that the Oligocene fossil is apparently identical with a species living to-day in the Himalayas, indicating that one form of the genus, at least, has persisted unchanged for a very long period of time. It is clear from this that the genus represents a very old type, and yet its floral organisation may be called, on general criteria, comparatively advanced. In particular, it shows the rare conditions of modification of the petals into accessory fruit-dispersal structures, a point of certain interest to students of Angiosperm phylogeny.

The discontinuity of Coriaria *in the southern hemisphere*

The discontinuity of *Coriaria* in the southern hemisphere is a close parallel to the discontinuity in the northern, and it further seems that it can be attributed to a similar cause. Allowing for the differences in land and sea distribution and for our less extensive geological knowledge of the southern hemisphere, the evidence for a Pleistocene glaciation there is as important as it is in the north. Whether the actual periods of maximum glaciation were simultaneous or alternating in the two hemispheres is uncertain, and not of great importance here, but the occurrence of a great glaciation comparable in severity with that of the north is undeniably shown. The parallel is further shown by the discovery within recent years of a fossil flora in Graham Land, that most northerly part of the Antarctic continent. This flora is of Tertiary Age and is direct evidence that the Antarctic, like the Arctic, supported before the Pleistocene a vegetation of warm temperate facies(35).

Here the parallel with the north ceases because the detailed effect of glaciation must have been very different. This is chiefly because the Antarctic is a continental mass surrounded by water, and the Arctic is the reverse. Hence, in the south, the northward migration made necessary by the advancing ice would everywhere encounter sea. In the direction of South America this water barrier is scarcely a serious one and very slight changes in level would tend to lessen it still more, but in the direction of New Zealand the barrier is much more serious. At present it is over 1000 miles wide and with an average depth of the order of 1000 fathoms. Such a barrier must be practically complete to anything but purely accidental dispersal. In the direction of South Africa the sea barrier is, of course, very much wider even than this.

In accordance with the lie of the land and sea masses of the southern hemisphere the general features of discontinuity there are simpler than in the north. Only two main types are distinguishable (36). The larger is that of discontinuity between temperate South America and temperate Australasia (in particular New Zealand); the smaller is discontinuity between temperate South Africa and Australasia (in particular Australia). In both the Australasian element tends to spread into Malay and Polynesia. There is no comparable relationship between the temperate floras of South America and South Africa. This points clearly to the fact that the present South American-Australasian floral element marks the remnant of former continuous

distributions across the Antarctic continent, a state of affairs ante-dating the Pleistocene.

In *Coriaria* there seems little doubt that the present southern distribution is the result of the modification by climatic change of a more or less continuous distribution between New Zealand and South America in the early and middle parts of the Tertiary. The main reason for this belief lies in the probable effect of glaciation in the southern hemisphere. Assuming for a moment that the features of land and sea were, at the beginning of the Pleistocene, what they are to-day, the effect of the oncoming ice would have been to drive the vegetation northwards in all directions towards a sea barrier. The whole Angiosperm vegetation of the Antarctic continent must have been exterminated, and indeed to all intents and purposes has never returned. But did any of it escape and become established elsewhere? Perhaps a few fortunate types may have crossed to South America; but even here there must have been great decimation, while it is difficult to see how any single type escaped towards New Zealand. It seems reasonable, therefore, to consider that the Pleistocene glaciation in the southern hemisphere swept away the flora of Antarctica leaving no trace there and causing considerable extermination of plant types. As affording possible evidence in support of this, it may be mentioned that the flora of temperate South America is poorer than that of any other region of similar distance from the equator either in the north or south, and it may be that this flora represents the descendants of those types which did escape the glaciation by migration into South America.

The discontinuity of Coriaria between the northern and southern hemispheres

It has been shown above that the discontinuities of *Coriaria within* each hemisphere can be explained as a result of the great climatic changes of the late Tertiary period and that they can be considered as of comparatively recent and contemporaneous origin, but no such considerations are applicable to the discontinuity *between* the two hemispheres. Quite a different solution must be sought for this problem. The first question that arises is whether or not the present distribution of the genus represents the outcome of a former con-tinuous range—whether, in fact, the genus is monophyletic or poly-phyletic. The more orthodox view holds that it is monophyletic, and that its present range is due to the geographical divergence of the two parts of the genus from a single point or area culminating in their

structural differentiation and geographical segregation. The important question becomes by what path and in what direction this geographical divergence proceeded, and, in particular, where and when the tropics were crossed. But there is another possible view which supposes that the genus is diphyletic or polyphyletic, and that the different parts of it are merely the product of convergent evolutionary trends and have no direct phylogenetic relationship. They must of course have had a common ancestor at one time, but what this was and whether or not it was an Angiosperm at all is unknown. Presumably the only evidence which could prove such a history for the genus would be very complete palaeontological records in both hemispheres, and these are lacking. Whether or no this theory is applicable to *Coriaria* in particular, it cannot reasonably be supposed to account for the many other similar cases of discontinuity in the Angiosperms and, moreover, it runs counter to all more generally accepted ideas of phylogeny and evolution. This point of view is not elaborated further here because its acceptance would automatically remove the necessity for any further discussion, and, until there is direct evidence to the contrary, *Coriaria* is assumed to be monophyletic and to have arisen once only at a definite part of the world's surface. This being so, the genus may have arisen either in the north and spread to the south, or in the south and spread to the north, or intermediately in the tropics and spread in both directions.

This problem of discovering the point of origin of a plant group is a common one in plant geography, and it not infrequently happens that a detailed study of the existing distribution assists greatly in deciding the direction of migrationary movement or geographical spread which, in turn, indicates the point of origin. Especially is this so when the group under discussion is discontinuous, and when its isolated parts show a close and orderly correlation between structural modification and geographical position: in short, when gradually increasing distance from some particular point goes hand in hand with gradually increasing morphological modification. The genera of Stylidiaceae afford an example of this[35]. In *Coriaria*, however, there is little or no help to be gained in this way. There are no intermediate structural forms connecting the sub-genera and there is scarcely any significant difference between the species composing each. Moreover, the plants at the most nearly adjacent points of the two hemisphere ranges are as unlike as they are at any other two points, while the plants at the extremities of each hemisphere range are practically identical. The plants of the Philippines and of New

Guinea are as unlike as those of Japan and South America, or as those of Europe and New Zealand, while those of Europe and Japan are almost, and those of South America and Fiji are quite, conspecific.

It may indeed be said that the occurrence of the genus in the Philippines and New Guinea represents some degree of geographical bridging between the two hemispheres, but a more careful consideration indicates that this is deceptive. The great differences between the two species concerned and the entire lack of intermediates is against this view. There is also no apparent reason for differentiating between the occurrences of the genus in New Guinea, Fiji and Samoa, and it is unlikely that the two last are remnants of a trans-tropical passage. The distribution, too, in the Philippines is copious over a very well-defined area, and has not the appearance of a relic distribution. At the same time, these points in no wise preclude the possibility of the trans-tropical passage having occurred in eastern Asia, but merely indicate that the present state of affairs is not a direct evidence or result of it. It appears more likely that the comparative proximity between the Philippines and New Guinea is due to subsequent geographical convergence.

The very difficulty of enlisting the help of the present distribution to decide the origin and movements of *Coriaria* is, in itself, significant. Since there are neither geographical nor structural intermediates between the hemispheres, it seems clearly indicated that the actual passage from one to the other must have occurred in the far distant past, a past so far distant that the subsequent lapse of time has effaced all evidence of the movement. Besides this, the climatic changes of the late Tertiary could only have produced the postulated effects upon distribution by their action on already widely diffused floras, a condition itself indicative of considerable passage of time.

Against these arguments it may be urged that the present distribution of *Coriaria* in America actually shows a passage across the equator in progress. But here again the circumstances are, in detail, very like those already described for the old world. The American mountain chain *may*, certainly, represent the path by which the genus passed from one hemisphere to the other, but there appear to be good reasons for believing that the present range in this part of the world is a subsequent and secondary development and thus represents a second and later tropical crossing. It will be noticed, for example, how the range stops at the northern end of the Central American mountains, indicating that in this direction the

genus has occupied all the suitable area. The genus is also entirely absent from the United States and Canada. Such a gradual and definite attenuation of range in a direction away from the bulk of related species and its marked topographical restriction indicate that it is the result of a spread from south to north and is comparatively recent. Were it otherwise and were North America the ancestral home of the genus, it is very strange and significant that it has left no relics there, either in the form of isolated endemics or as fossils. It should be clearly understood that by "comparatively recent" is meant at a time subsequent to the original crossing of the tropics, which may have been early Tertiary. Incidentally, it seems reasonable to ascribe both the new and the old world presumed secondary extensions northwards directly or indirectly to the effects of the late Tertiary glaciation in the southern hemisphere.

These considerations dispose of the only aspects of *Coriaria* which seem as if they might help in deciding its original home, and the only remaining course is to weigh up and compare the three possibilities mentioned above. But whichever of these is taken, one and the same difficulty arises. Throughout the range of the genus there are varyingly wide areas of sea separating the component areas, and it very soon becomes apparent that unless casual dispersal between them is invoked the present distribution of *Coriaria* can only be explained by supposing that great changes in the distribution of land and sea have taken place during its history. This is a highly important realisation, reached not only by the study of *Coriaria* but also from a general survey of the geography of the Angiosperms. It is so important that it must be discussed at some length, but first some remarks must be made about what has just been called "casual dispersal."

This may be defined as dispersal which can only be successful under particular or peculiar circumstances; *or* as dispersal which transports a fruit or seed far beyond the flora to which the parent plant belongs, so that establishment among a quite different assembly of species has to be accomplished before the dispersal can be effective. It includes accidental introduction and carriage by man (although here the difficulties of establishment are usually modified), exceptionally wide dispersal by wind, dispersal on or in floating bodies and, particularly important in the present discussion, exceptionally wide dispersal by animals (chiefly birds). The suggestion of the dispersal of *Coriaria* fruits, with their fleshy and edible floral parts by birds is, indeed, possible and therefore it is a facile hypothesis that the discontinuity of the genus is wholly or in part due to such cause.

But, just as in discussing the possible polyphylogeny of the genus, it can be said here that, while such an explanation may hold for certain details of the distribution, it is most unlikely to account for all the discontinuity and certainly cannot explain all the other numerous similar discontinuities. As a general hypothesis of distribution it clearly cannot replace that of changes in land and sea configuration, which has now to be discussed.

THE PROBLEM OF CHANGES IN THE DISTRIBUTION OF LAND AND SEA

For the plant geographer, hypothetical changes in the outline of land and sea must clearly be such as may have sufficed at some period to bring into direct communication the now scattered land masses of the world. It is not necessary that such communication should have been everywhere contemporaneous, but, since Angiosperms are under discussion, it is necessary to assume that they occurred during or since the Later Cretaceous. Such communications can be visualised in two quite distinct ways. It may be supposed that the positions of the present land masses are considered to have persisted unchanged but that, at some period, other land masses, now disappeared, formed bridges between them. This may be called the theory of land bridges. Or it may be supposed that the present land masses were once in actual contact, and that subsequent divergent horizontal movement has separated them widely. This may be called the displacement theory.

The position of the land-bridge theory among scientific hypotheses is rather peculiar. It seems not to be based upon any very definite direct evidence, except perhaps certain features of oceanic orography, but rather to be the natural corollary to a belief in the permanence and immutability of continents and oceans. This conception itself has acquired a deceptive infallibility because, until recent years, it has never been seriously challenged, and has largely become accepted without question. The frequent occurrence of marine sedimentary beds far inland perhaps has a bearing on the theory, but, while they unquestionably indicate great changes in coast-line as well as in level, they do not necessarily indicate the former existence of land where now are oceans. In fact the very characters that identify such beds as marine, clearly identify them as deposits in the comparatively shallow water of epicontinental seas. The opposite kind of evidence, that of the occurrence of land or fresh water deposits where there are now deep seas, does not seem to be known at all. Despite lack of direct evidence, the land-bridge theory has become very widely

established in absence of an opposing theory, and therefore has all
the forces of conservatism on its side, but there are, nevertheless,
good reasons for considering it inadequate to explain Angiosperm
distribution.

In the first place, it is not generally realised what support of this
theory involves or to what extent land-bridges must be invoked. It
is needless to specify the numerous land connections necessary to
explain all the spatial relationships between Angiosperm floras, but
it is probably no exaggeration to say that they would include land
bridges across almost every sea and ocean, a result which, apart from
anything else, would almost cover the globe with land. The geo-
graphical affinities of the floras of such regions as Hawaii and the
Southern Oceanic Islands are cases particularly in point. But even
this might be acceptable if it was permissible to imagine the bridges
produced and existing at very different stages in geological time,
only a few being contemporaneous. This, however, is not possible
because the Angiosperms appear not to have been abundant until
the latter few of the Lower Cretaceous, and any bridges capable
of affecting their distribution must have existed since that time.
Considering these difficulties, it seems doubtful if any geologists
would be prepared to postulate the desired number of bridges in the
time allowed. It is easy to suggest a single land bridge to explain a
single geographical affinity, but it is quite another matter to suggest
all the land bridges required to explain all geographical affinities.

It may be urged that chains of islands would be as effective in
assisting plant distribution as continuous land surfaces. This may,
indeed, be true for those plants which are capable of prolonged
transport as seeds or fruits, but there is no reason to suppose there has
been any marked selection in favour of such types and, in order to
allow the migration of the much more numerous plants of average
dispersal potentiality, the individual islands would have to be so
many and so closely spaced that the result would be almost a con-
tinuous land surface.

The great hypothetical continent of Gondwanaland could, it is
true, have supplied many of these bridges, but this great land mass
is generally supposed to have disintegrated in the Cretaceous or very
early Tertiary, certainly at a time which much reduces its usefulness
in the present connection. This disintegration is supposed to have
occurred by the foundering of various parts of the mass and this
leads to another point against the land-bridge theory. If foundering
was the usual cause of disappearance of bridges, as it presumably

was, it is at least surprising that of all the oceanic islands scattered over the globe, scarcely any bear any trace of sedimentary rocks. None of them appear to be the direct remnants of continents, although some of the volcanic material of which they are composed may have had such an origin. If they are indeed continental remnants their general volcanic nature is at least peculiar.

Another point connected with the foundering of land especially concerns the plant geographer. In order that such foundering shall result finally in widely discontinuous distributions, either the group of plants concerned must exist from end to end of the land destined to sink, or else the foundering must proceed in so convenient a way that divergent migration towards persistent land surfaces is possible. The former assumes and requires rather exceptionally wide specific or generic ranges, while the latter has obvious difficulties. In general the necessary divergent migration could only result from a sinking which originated in the centre and spread gradually towards the extremities of the land mass concerned. At the same time it must be remembered that modern discontinuities represent only the survivors of such sinking, and give no indication as to the amount of extinction that may have occurred.

With the general conception of continental displacement as opposed to land bridges Wegener's theory [32] is particularly associated because it was the publication of this which first put into effective and unmistakable words the growing tendency towards a hypothesis which would envisage the possibility of continental movement. Other theories have subsequently been developed, but it is convenient to begin with a discussion of this special theory. Wegener postulates that previous to the Carboniferous the land masses making up the present continents were closely grouped into one huge continent centred about what is now Africa, but that towards the end of that period this continent began to fragment and the portions to drift apart, Africa remaining unmoved. This divergent drift is supposed to have continued ever since, and to have resulted in the arrangement of the continents as seen to-day, but the individual continents are thought to have separated successively and not simultaneously. For example, the separation of America from the old world originated in the south, and has only comparatively recently extended to the extreme north. Associated with this main theory is a secondary hypothesis of pole movement which seeks to co-ordinate what is known of the past climates of the world.

The evidential basis of Wegener's theory is largely derived from

four sources, of which the chief are the peculiar and often correlated shapes of separated land masses and the similarity between the geological formations on both sides of certain oceans, notably the Atlantic. Subsidiary lines of evidence are features in the distribution of animals and plants and the indication that the longitude of certain places, e.g. in Greenland, is increasing. This last evidence is not altogether satisfactory.

Contrasted with the theory of land bridges the hypothesis of displacement attributes the separation of continents to displacement or drift rather than to the foundering of intervening land. It is important to note that either theory permits the postulation of a Gondwanaland, but that in the latter the disintegration is dated as commencing much earlier.

The Wegenerian theory would seem from this brief consideration to compare very favourably with that of land bridges as a working hypothesis to explain flowering-plant geography, but unfortunately the forces which the author of the theory invokes as causes of displacement are considered by most geophysicists to be totally inadequate. In addition to this, the original exposition of the theory was made in very great and, it will be generally agreed, unnecessary detail, so that it was laid open to overmuch minute criticism. For example the author postulated a very complete chronological sequence of events, which can scarcely be accepted wholesale, and which tends to discredit the central thesis of displacement as opposed to immutability.

The position with regard to these theories is that while the general idea of land bridges seems untenable, the opposing view of displacement according to Wegener is likewise unacceptable for certain definite reasons. Hence it seems that a theory of displacement modified to remove these special disabilities would provide a general hypothesis by which, in combination with certain other factors such as climatic change, the distribution of flowering plants as a whole could be explained. Any thesis likely to pave the way towards this goal is clearly of importance to the plant geographer.

For this reason the theory of recurring cycles, recently elaborated by Professor Joly, although not a displacement theory, has several significant features. As with Wegener, the physical basis of this theory is the conception of the continents as composed of a less dense sial supported upon a more dense sima—a conception now generally accepted—but the details are quite different. It is supposed that the sima is normally solid for an immense depth, and that during

vast passages of time its temperature gradually increases by the accumulation of the heat produced by the disintegration of the radioactive substances within it. With this accumulation of heat the sima progressively becomes molten towards the surface until the point is reached when the still solid crust is so thin that there is great escape of the contained heat, especially into the ocean basins. This escape of heat and consequent cooling of the sima continues until the whole solidifies once more and the cycle recommences. During the "molten" phase—when the solid sima crust is thinnest, the general density of the sima is lowered and the continents undergo depression relative to the average sea bottom, with the result that epicontinental seas tend to be widespread. With the re-solidification of the sima and its consequent increase of density the continents are re-elevated and the epicontinental seas ebb. It is supposed further that stresses are set up chiefly as the result of the expansion of the sima, so that at some stage in each cycle considerable mountain building occurs. About seven such cycles are thought to have occurred in geological time, the most recent being of Tertiary date and correlated with the Alpine orogeny.

It will be seen that the theory makes no mention of continental drift, nor does it seem likely that such could result in any significant degree in the circumstances described. It does, however, visualise a complete slipping of the sial and solid sima over the molten sima core under tidal influence and a possible differential movement of individual sial masses, but only of insignificant dimensions.

For the plant geographer this theory is of value for two reasons, first because it allows for the observed changes in level of the continents and secondly because it dates a complete cycle in the Tertiary —during the phylogenetic history of the Angiosperms. If, under the theory, very considerable displacement could be admitted, then it would, in association with other factors, provide an adequate explanation of the facts of plant distribution and palaeogeography. The crux of the matter lies in that part of the theory which supposes that the sima never becomes completely molten, but that a thin solid crust persists under the oceans so that horizontal displacement is impossible.

Any further reference here to geophysical theories is clearly undesirable, but there seems increasingly little doubt that before long a theory of continental movement, free from the weaknesses and objections of those existing, will be elaborated. The essential features of such a theory, to the plant geographer, must be the hypothesis of

considerable continental drift in the time since the rise of the Angiosperms and the orientation of such drift so as to account for much of the marked spatial relations between widely separated Angiosperm floras, particularly those of the southern hemisphere.

SUMMARY

1. The genus *Coriaria* is the only genus of the Coriariaceae, a family of polypetalous dicotyledons of very uncertain systematic position but probably finding a place in or near the Celastrales.

2. The species are woody plants, varying in size from undershrubs to small trees, with entire 3-veined leaves, and small flowers borne in racemes.

3. The genus is much in need of taxonomic revision, but this can only be done adequately by detailed field study. It is, therefore, not possible to say exactly how many species it contains.

4. It is possible to divide the species into three sub-genera distinguished by conspicuous characters apparent in nearly all dried material.

5. A number of fossils have been ascribed to the genus. One, a complete fruiting branch from the Oligocene of south France is of special interest and importance. It is indistinguishable from a species now living in the Himalayas.

6. The distribution of the genus is markedly discontinuous. It is found in: (*a*) the western Mediterranean; (*b*) in continental and insular eastern Asia; (*c*) in New Zealand and other parts of Australasia; and (*d*) in western South America and in Central America.

7. Of the sub-genera, two are confined to the northern hemisphere (one in the Himalayas only), the third is confined to the southern hemisphere.

8. The discontinuity of the genus is discussed at length and it is suggested that discontinuity normally marks the geographic and phylogenetic senility of a genus. The main types of generic range are noticed, reflecting respectively juvenile, mature and senile conditions in the plant group concerned.

9. The discontinuity *within* the northern hemisphere is attributed to the great climatic changes which culminated in the glaciation of the late Tertiary.

10. The discontinuity *within* the southern hemisphere is attributed to the same cause.

11. The discontinuity *between* the two hemispheres can only be explained on the assumption of great changes in the distribution of

land and sea during the past. The two theories of land bridges and continental displacement are considered and it is concluded that the latter is the easier and more satisfactory explanation.

12. Certain geographical theories are shortly described and the opinion is expressed that while at present there is no acceptable hypothesis of displacement, such will be forthcoming before long and that the geography of the Flowering Plants will afford important evidence in its support.

The writer is indebted to Dr A. B. Rendle of the British Museum (Natural History) and to the Director of the Royal Botanic Gardens, Kew, for the facilities afforded for the examination of specimens, and to the Officers in charge of the herbaria in Berkeley (Cal.), Berlin, Brisbane, Brussels, Calcutta, Cambridge (Mass.), Chicago, Copenhagen, Edinburgh, Geneva, Melbourne, Ottawa, Paris, Rome, St Louis, South Yarra, Sydney, Tokyo, Vienna, Washington, Wellington and Zurich for particulars of the specimens of *Coriaria* in their collections. From Professor A. C. Seward the writer has gratefully received many valuable comments and criticisms, especially upon the more geological aspects of the paper. Thanks are also due to Professor J. Joly for assistance in elucidating points in connection with the theory of recurring cycles.

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THE DEVELOPMENT AND STRUCTURE OF THE SEEDLING AND YOUNG PLANT OF THE PINEAPPLE (*ANANAS SATIVUS*)

By E. N. MILES THOMAS, D.Sc., F.L.S., Fellow of Univ. Coll. Lond., and L. E. HOLMES, B.Sc.

(With 31 figures in the text)

DURING a visit made by one of us to the Hawaian Islands, following upon the meeting of the British Association held in Toronto in 1924, interest was aroused in the pineapple plantations and the question of securing seed and seedlings of *Ananas sativus* was raised. Several years later material arrived rather unexpectedly, sent by Professor Bergman of the University of Hawaii, and an investigation was begun.

The object of the investigation was to follow out the early stages of development of a plant of such commercial importance and to compare with similar stages of hybrids when obtainable. These are being raised by the Association of Pineapple Growers, who have very kindly been forwarding the requisite material as soon as it becomes available.

Nothing of outstanding interest has eventuated as yet, but in view of the paucity of the literature on the subject it seems worth while placing on record a detailed description of the morphological and anatomical development from the germination of the seed to the establishment of the young plant during the first year of its life.

In the account given by Dr Killerman[1] of the history of pineapple discovery and culture it is stated that its American origin is undoubted, as, although cited from Bengal in the sixteenth century, no Sanskrit name is known and it probably was brought from Guadaloupe to Europe first by Columbus at the end of the fifteenth century. Cultivation seems to have started in the greenhouses at Leiden in the middle of the seventeenth century and in England in the eighteenth century. Propagation by suckers is spoken of by Weinmann, a botanist of Regensburg, but seed would appear not to have been germinated. Five or six species are known, of which *Ananas sativus* is the most important, and some sixty kinds.

Hybrid material of several crosses between the Pernambuco,

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[1] S. Killerman, *Naturwissenschaftliche Wochenschrift*, Sept. 1918.

Guatemala, Cayenne, and Tabuga varieties have been received and examined, but this part of the work is not complete and publication is reserved.

We have been successful in raising plants from seed in the Botany Department of University College, Leicester, both of the original *Ananas sativus* (the oldest of which are now about 18 months old) and of the hybrids subsequently received.

The seeds of the strain of *Ananas sativus* customarily cultivated in Hawaii were examined in the resting condition and were germinated according to suggestions received with the seeds. The seedlings and young plants, in various stages of development, were fixed in Merkel's fluid and later were embedded and microtomed, the sections being stained with Bismarck brown and gentian violet. Some of the plants were allowed to continue their growth in pots and are now about 18 months old.

A. THE SEED

External features

The seed of the pineapple in the resting condition is a small body about 4–5 mm. long and 2 mm. broad. It is a dark chocolate brown in colour. The shape is roughly that of one-half of an egg which has been cut in two longitudinally, one of the broad surfaces being flat and the other curved (Fig. 1). The more pointed end of the seed is very often lighter in colour than the rest of the seed. The testa is extremely tough and leathery and has numerous ridges running longitudinally down it.

Internal features

Within the testa the seed consists of (*a*) a mass of endosperm, and (*b*) a minute embryo situated at the more pointed end of the seed.

The testa is very thick and in section is found to consist of three layers; an inner layer of very dark brown, much thickened cells, a middle layer of lighter brown cells and an outer one of yellowish-coloured cells (Fig. 2). The innermost of these layers is of more or less uniform thickness in all parts, as is also the outermost layer, but the varying thickness of the middle one causes the ridges and furrows on the outside of the seed. This layer consists of groups of large cells alternating with groups of small cells. The ridges caused by these cells show very clearly in transverse section (Fig. 2 *a*, *b*). The cellular structure of the inner and outer layers is more apparent in longitudinal than in transverse section, it being practically impossible to distinguish the separate cells of these layers in a transverse

section. Towards the apex of the seed the outer cells develop from their external walls yellowish hairy outgrowths of a cuticular nature which cause this part of the testa to appear of lighter colour than the rest (Fig. 2 *a*).
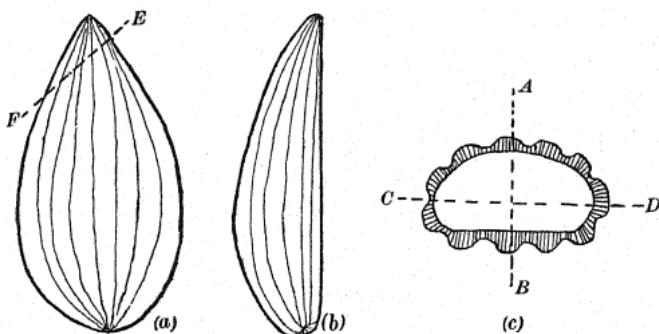
Fig. 1. Pineapple seed (×about 256). (*a*) Front view. (*b*) Side view. (*c*) Transverse section through middle of seed.
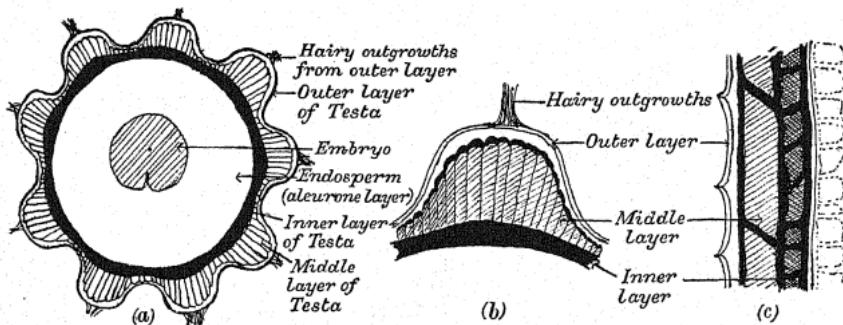
Fig. 2. Structure of testa. (*a*) T.S. of seed near apex. (*b*) T.S. of one ridge. (*c*) L.S. of part of testa.

The endosperm consists mainly of a mass of thin-walled cells surrounded by a layer of smaller cells, which is one cell deep except in the neighbourhood of the embryo, where it increases so that it is several cells deep. This is the aleurone layer and the cells contain numerous small granules which give the usual protein reactions. The main mass of the endosperm is composed of large cells packed with oval starch grains which, on taking up water, become polygonal by mutual pressure. Millon's reagent and the Biuret test

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show that there is also a little protein present in these cells in the form of minute grains packed between the larger starch grains (Fig. 3).

Large Endosperm cells with starch grains & protein granules

Aleurone layer

Fig. 3

Position of Plumular growing point

Outer surface in contact with aleurone

Inner surface in contact with starchy endosperm

(a)

(b)
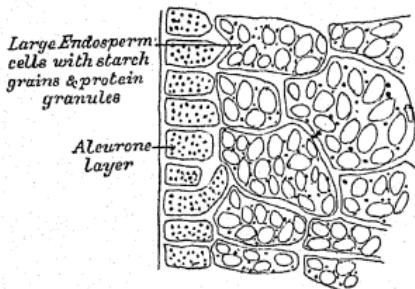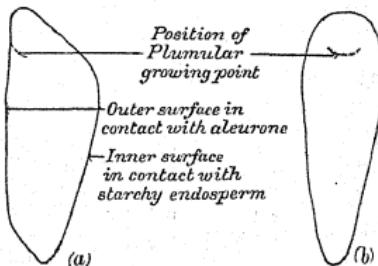
Fig. 4

Fig. 3. Section through part of endosperm.
Fig. 4. Detached embryo. (a) Surface towards flat side of seed. (b) Surface towards narrow side of seed.

Hairy outgrowths from Testa

Plumular growing point

Longitudinally elongated cells

Isodiametric cells

Aleurone layer

Starchy cells

Testa

Embryo

Plumular growing point

Longitudinally elongated cells

See fig.7

Starchy cells

Aleurone layer

Testa

Cell walls forming division line down centre of endosperm
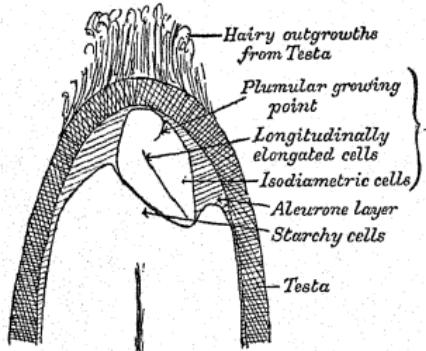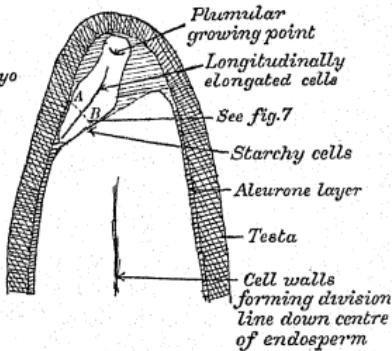
Fig. 5

Fig. 6

Fig. 5. L.S. of upper part of seed cut parallel to flat surface.
Fig. 6. Upper part of seed cut obliquely at right angles to flat surface with embryo in L.S.

Down the centre of the endosperm is a division line caused by partially collapsed cells whose walls become pressed together giving a darkish region between the two halves of the endosperm (Figs. 5 and 6).

The embryo when detached from the seed appears as a minute, more or less cylindrical structure, but slightly more pointed at one

end than the other. Viewed from the side, it is angular on the inner surface in contact with the starch-containing cells and nearly straight on that showing the plumular groove and lying against the testa, in contact with the aleurone cells.

The embryo lies obliquely across the pointed end of the seed with its narrower end towards the inside, and its blunter end, which proves to be the radicle, directed externally and nearly filling the pointed apex of the seed. The embryo only comes into contact with the starchy cells of the endosperm on about one-third of its surface: the rest is surrounded by the aleurone layer which, as mentioned above, is several cells thick in this part. The embryo lies practically wholly in one-half of the seed, when the seed is cut in half longitudinally at right angles to the flat surface. Median longitudinal sections of the seed can obviously be made in two planes, at right angles or parallel to the flat surface (*AB* and *CD* in Fig. 1 *c*). Longitudinal sections of the seed cut at right angles to the flat surface (i.e. in plane *AB*, Fig. 1 *c*) do not pass longitudinally through the embryo but cut a limited portion of it in an obliquely transverse manner. In order to obtain longitudinal sections of the embryo it is necessary to cut the seed in a plane parallel to the flat surface (*CD* in Fig. 1 *c*) or else obliquely (in plane *EF* in Fig. 1 *a*).

The longitudinal sections of the embryo show that the growing point of the plumule is situated very near the rounded or radicle end of the embryo, and on the side away from the protuberance, or angle mentioned above.

In the soil the seed will presumably tend to lie on its flat surface, in which case the growing point will be towards the upper side of the embryo.

In longitudinal section the embryo is found to consist mainly of regular, isodiametric cells with the exception of the innermost cells. These central cells are elongated in a longitudinal direction and are evidently the elements destined to form the vascular tissue of the seedling when growth begins, and they extend through most of the cotyledon from the tip to a short distance from the plumular growing point. All the cells of the embryo are filled with reserve food materials. Microchemical tests show that these consist of minute granules of protein, together with a little starch and a considerable quantity of oil.

B. GERMINATION

The seeds were treated according to suggestions received from Hawaii. They were first of all sterilised by being dipped quickly into absolute alcohol, and then into strong sulphuric acid. They were then thoroughly washed in distilled water until quite free from acid. The apparatus used was also well sterilised by washing with a dilute solution of mercuric chloride. Two glass dishes of the form of a large Petri dish were used. The top of the smaller dish was covered with sterilised cotton wool and inverted inside the larger one. The sterilised seeds were spread out on top of the cotton wool, and distilled
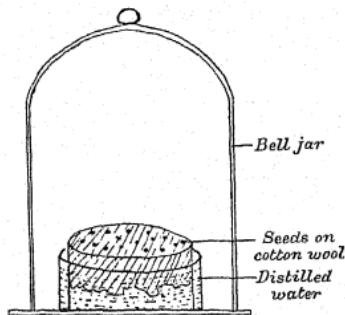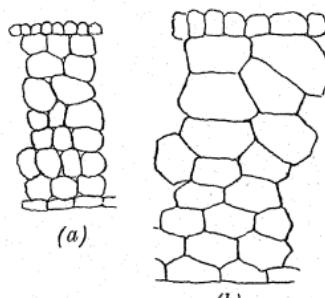
Fig. 7. Apparatus used to germinate seeds.
Fig. 8. Part of L.S. of cotyledons to show expansion of individual cells which causes emergence of radicle end of embryo. (a) From resting seed. (b) From seed commencing to germinate.

water poured over them until there was enough in the outer dish to cover the ends of the cotton wool and so keep it moist. The whole was placed on a glass plate and covered with a bell jar to ensure a moist atmosphere (Fig. 7). The apparatus was then placed in the greenhouse and kept at a temperature of about 75°–80° F. This temperature was found to be the best at which to germinate the seeds.

Temperatures much lower than 75° F. delay germination too long, resulting in many cases in the rotting of the seeds. Submission to a temperature of 75°–80° F. induces germination in about 3 weeks. For example, those sown on January 28th had started to germinate by February 18th, but at 60°, the first temperature used, none of the seeds germinated in less than 3 months and many of them took as long as 6 months, while about 20 per cent. of them rotted away.

Keeping the seeds for a considerable length of time does not seem to have an adverse effect on their germinating power, as seeds which had been kept for about $2\frac{1}{2}$ years still germinated within 3 weeks.

The seedlings were not removed from the apparatus shown in Fig. 7 until about 3 months from the time of sowing, when they were planted out in pots in leaf mould. Those which have been allowed to continue their growth are now about 18 months old, and are still quite healthy and are adding to their size.

When first placed in the germinator the seeds soon swell considerably (in the course of a day or so) in the damp atmosphere, but the first indication of germination is the splitting of the testa at the more pointed end where the hairs make it lighter in colour. The radicle end of the embryo then begins to emerge. The emergence of this end seems to be largely passive and to be due to the elongation of the other, i.e. cotyledonary, end of the embryo by expansion of the cells of the cotyledon (Fig. 8). Immediately after the appearance of the radicle a small lump is seen on the upper surface of the growing embryo. This is the plumular growing point. The radicle now grows rapidly and soon turns downwards at right angles while the plumular growing point bursts through the cotyledonary sheath and small plumular leaves appear and soon turn green. The leaves arise with practically no internodes and the stem is extremely short, with the result that the habit of the plant is very condensed. The cotyledon remains inside the seed as an absorbing organ. The primary root does not function for very long but, by the time two or three leaves have developed on the shoot, adventitious roots begin to grow out from the short stem at the base of the leaves and the primary root withers away.

From this time onwards no great change takes place in the form of the young plant. The leaves and roots increase in size and in number but the stem remains very short, the leaves being given off at extremely short internodes practically at the level of the soil. The phyllotaxy is found to be rather a complex one, the angle of divergence being about 220°, which gives a phyllotaxy of 11/18, but two-thirds may be taken as a rough approximation. As a rule, after the primary root has ceased to function, there is no dominant main root, several of the adventitious roots being of equal size and importance, but occasionally one of the adventitious roots may produce lateral rootlets (Fig. 9).
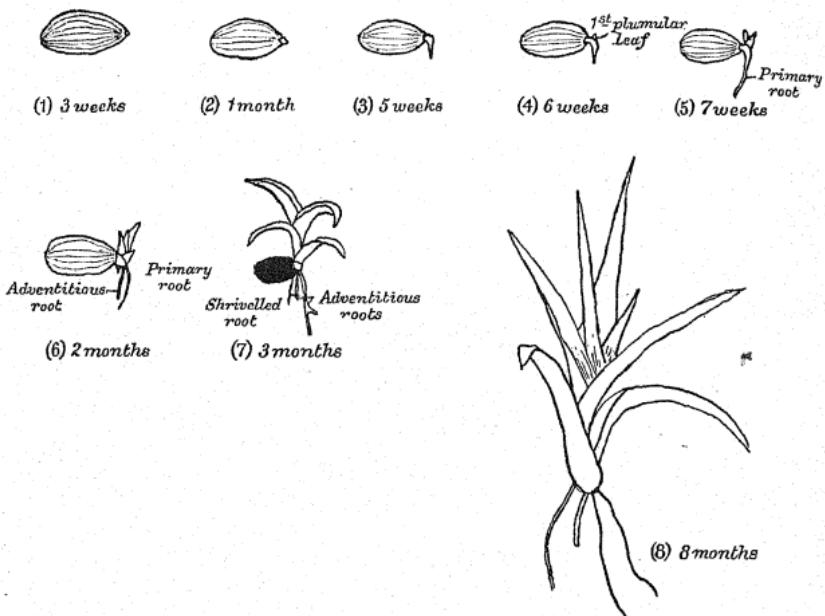
Fig. 9. Stages in germination.

C. Anatomy of Seedling

The internal structure of the seedling was investigated at three stages in its development. The youngest stage microtomed was that in which the radicle had only just begun to emerge from the seed coat—the seedling being about 3 weeks old (Fig. 9 (1)). At this early age the future vascular tissue can be recognised, but no lignification has taken place (Fig. 10).

The only plumular tissue present is the meristematic growing point which is enclosed in the chamber made by the sheathing base of the cotyledon. In shape the cotyledon is a more or less cylindrical solid plug, which becomes hollowed at the base in an asymmetrical manner so as to form a little conical chamber in which the plumule first develops. The wall of the chamber is thick on one side, and on the other consists of only a few cell layers with a slit through which the plumule ultimately emerges. The plumular growing point is situated very near to the blunt root end of the embryo, which is being pushed out of the seed but the cells of which have not yet

begun to elongate, the growth which causes the emergence taking place in the cotyledon.

In transverse section at the level of the cotyledonary node there are indications of two small groups of young vascular tissue in the centre, situated on the diameter which passes between the two arms of the cotyledonary sheath through the plumular bud and the thickest part of the cotyledon (distinguished as "leaf plane") (Fig.
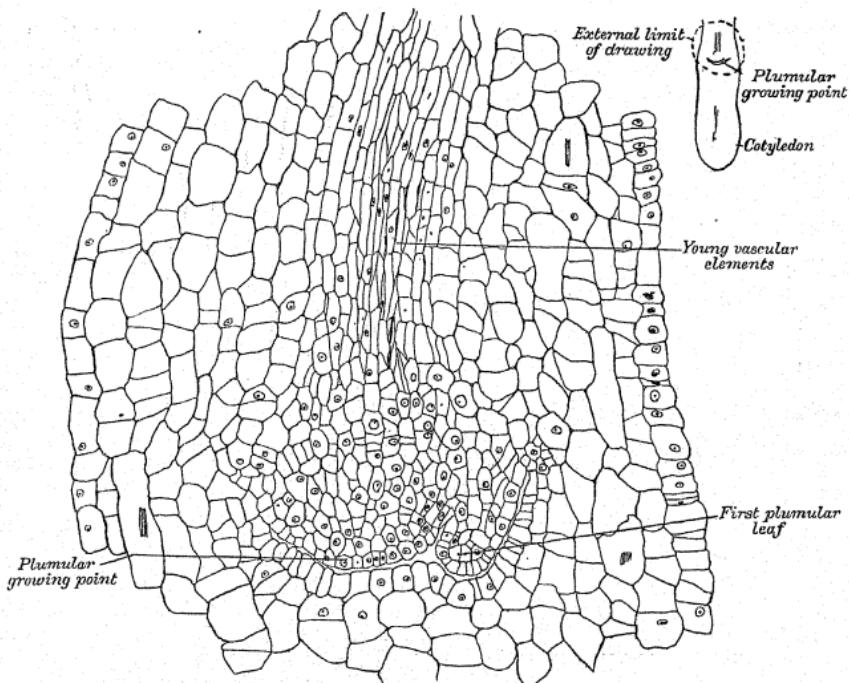
Fig. 10. L.S. of 3-weeks-old seedling showing growing point.

17 A (3)). Following the course of these two groups down into the root, the one nearest the plumular bud fades away first, followed a little lower down by the other (Fig. 17 A (1), (2)). Passing upwards they are to be distinguished through the greater part of the cotyledon, and only disappear a few sections below the tip. As they pass up the cotyledon these groups of young vascular tissue get closer together (Fig. 17 A (5)), until near the tip they are indistinguishable the one

from the other (Fig. 17 A (6)). At one point, about three-quarters of the distance between the cotyledonary node and tip, the group that is towards the plumular bud shows indications of the beginnings of lignification, showing that it is a young xylem group while the other group appears to be phloem. Thus differentiation of vascular tissue has taken place in the greater part of the cotyledon, but very little in the root.
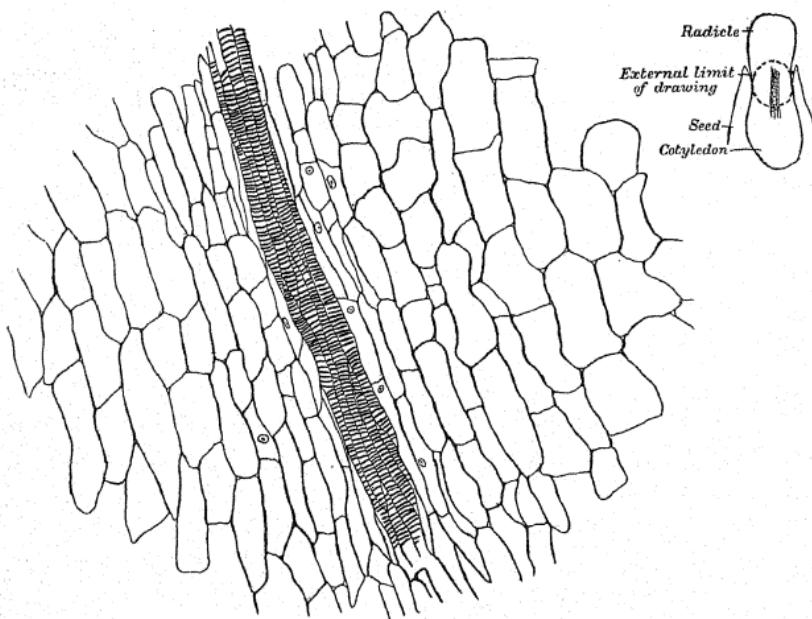
Fig. 11. L.S. of 4-weeks-old seedling showing xylem.

The cells of the embryo at this stage are still filled with food material with the exception of those of the growing point and round the vascular bundle.

A month-old seedling (Fig. 9 (2)), cut before the radicle has begun to turn down, shows considerable lignification (Figs. 11 and 12). Although externally the seedling has not altered very much, internally there is considerable advance. The plumule has developed one leaf, but it has not yet emerged from the cotyledonary sheath which meanwhile has considerably enlarged. Internally the cotyledon

possesses a group of phloem elements and a group of xylem elements
arranged collaterally so that the xylem faces the plumule. The posi-
tion of the first-formed xylem elements may be regarded as uncertain
at the base of the cotyledon (Fig. 13 *b*), but near the tip (Fig. 13 *a*)
the protoxylem is clearly to be recognised and it is seen to be
mesarch to exarch, that is towards the phloem side of the bundle,
while that of the plumular leaf is endarch (Fig. 13 *c*).
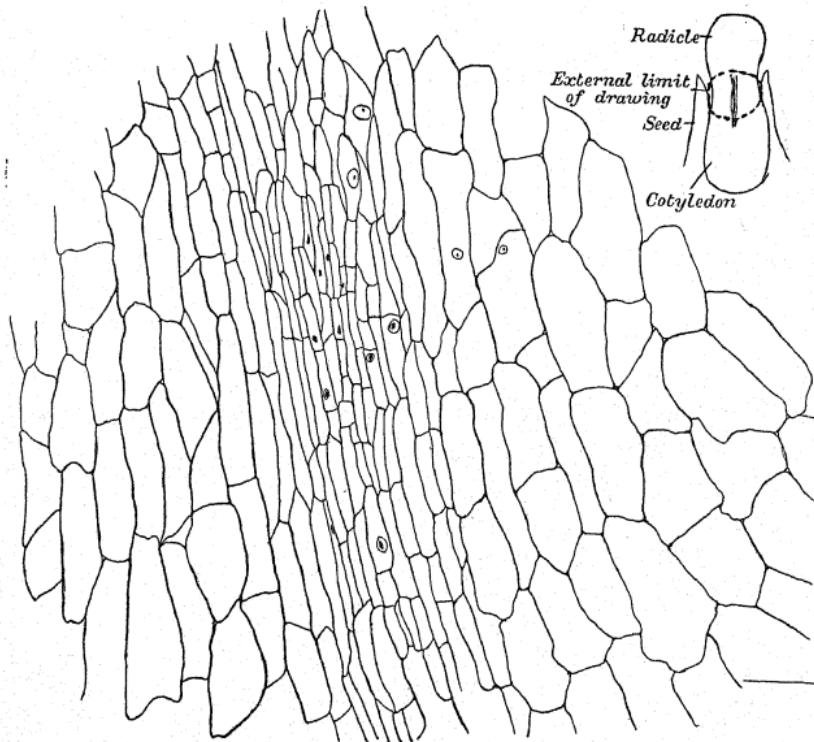
Fig. 12. L.S. of 4-weeks-old seedling showing phloem.

At the cotyledonary node the phloem group present in the centre
of the first plumular leaf passes in at right angles and appears at
the top of the short hypocotyl on the opposite side of the xylem to
the cotyledonary phloem group (Fig. 14). The number of xylem
elements decreases until at the top of the hypocotyl only two or

three remain and these become arranged in a plate (distinguished as "inter-leaf plane") immediately below the level of the cotyledonary node and, with the two phloem groups, one cotyledonary and one
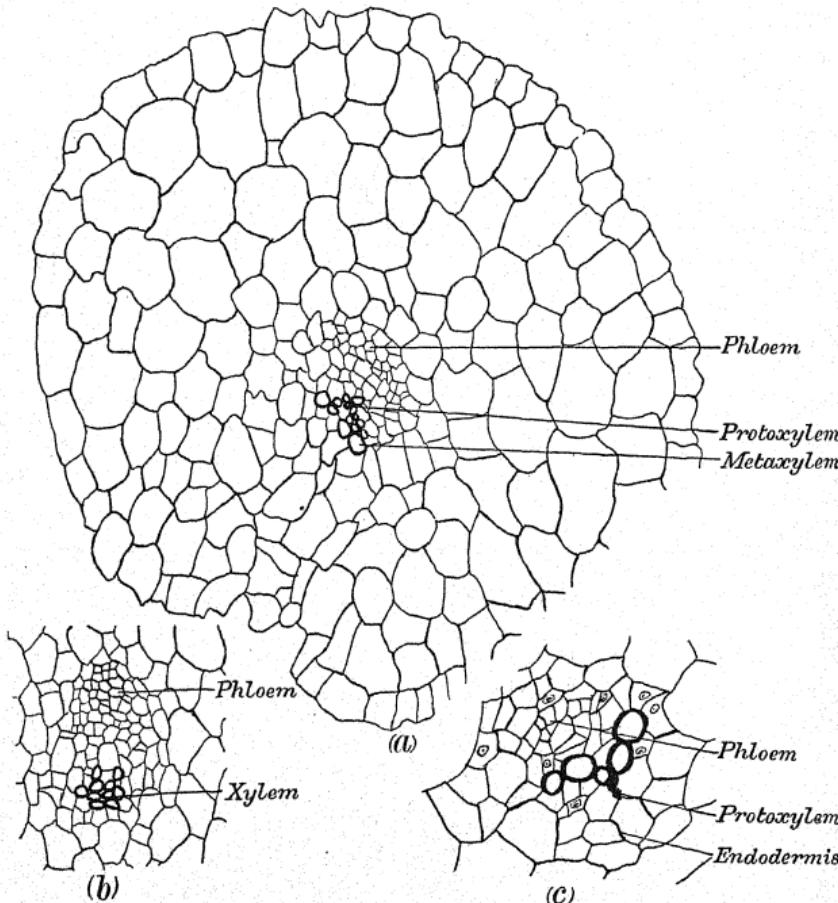
Fig. 13. (a) T.S. of tip of cotyledon of 4-weeks-old seedling. (b) Structure of cotyledonary bundle at base of cotyledon. (c) Structure of sole bundle of 1st plumular leaf of 2-months-old plant.

smaller plumular, they produce a diarch arrangement of the vascular tissues (Figs. 14 and 17 B (3). In this diarch structure the small xylem plate lies at right angles to the plane passing through the

cotyledon and the plumule ("inter-leaf plane"), while the phloem groups lie on that plane.

The hypocotyl is very short and soon passes into the root. A ring of endodermal cells appears round the vascular tissue and at a level only slightly lower root hairs are given off by the epidermal cells.
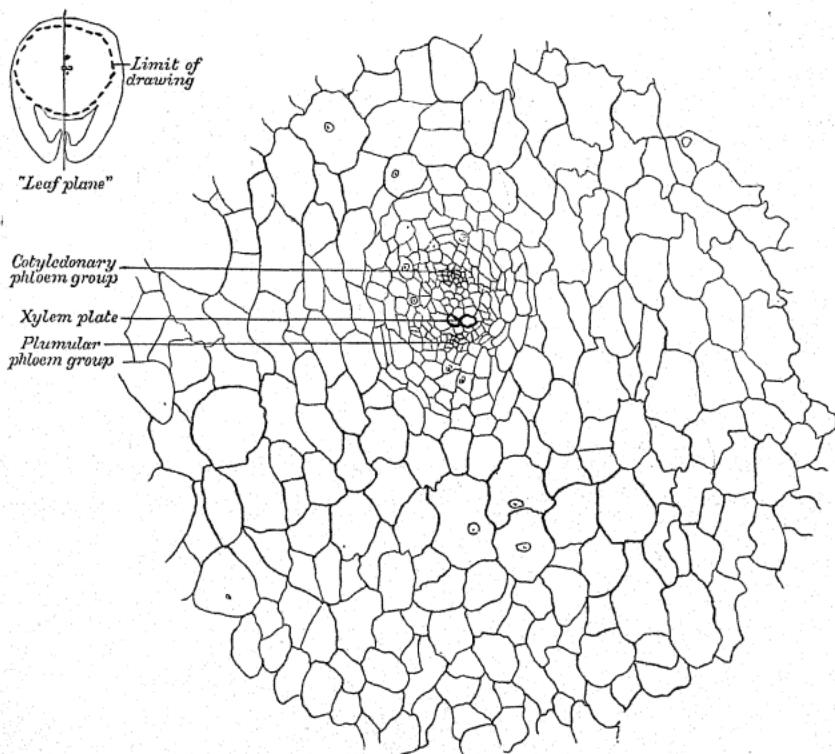
Fig. 14. T.S. of 4-weeks-old seedling just below cotyledonary node.

As we pass down into the root the xylem group splits up, forming about three or four small groups (Figs. 15 and 16), and later the phloem divides also. The result is the formation of a triarch or tetrarch root, the xylem poles in the tetrarch root being in the diagonal plane (Figs. 17 and 18). So short is the so-called hypocotyl that a section only 0·35 mm. below the actual cotyledonary node

(Fig. 17 B (3) shows the remains of the free cotyledon wings or sheath as well as root hairs and other root characters.

Thus, taking the vascular structures of the hypocotyl as consisting of a plate of xylem and two groups of phloem, one phloem group and apparently the whole of the xylem is continued upwards
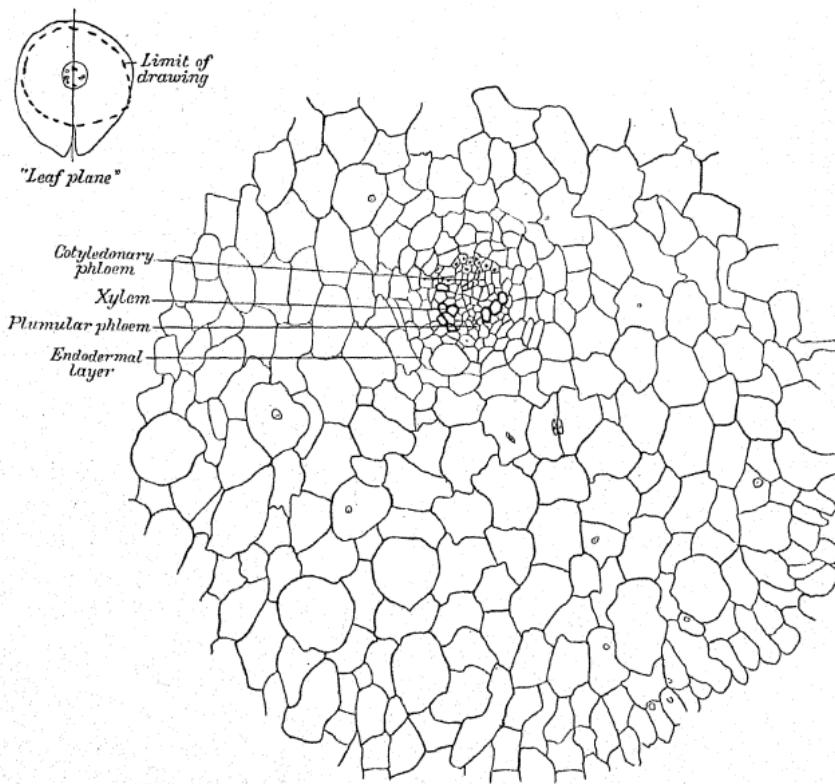
Fig. 15. T.S. of primary root of 4-weeks-old seedling.

through the cotyledon while the second phloem group is continuous with the vascular strand of the first plumular leaf.

The transition from cotyledon to root in *Ananas sativus* follows a very simple method, the single cotyledonary bundle forming a diarch structure with the aid of a plumular phloem group, this

giving way to a triarch or tetrarch structure in the later-formed part of the root.

The arms of the cotyledonary sheath possess some cells larger than the rest which contain raphides of crystals—bundles of needle-shaped crystals similar to those which will be described in the leaf.
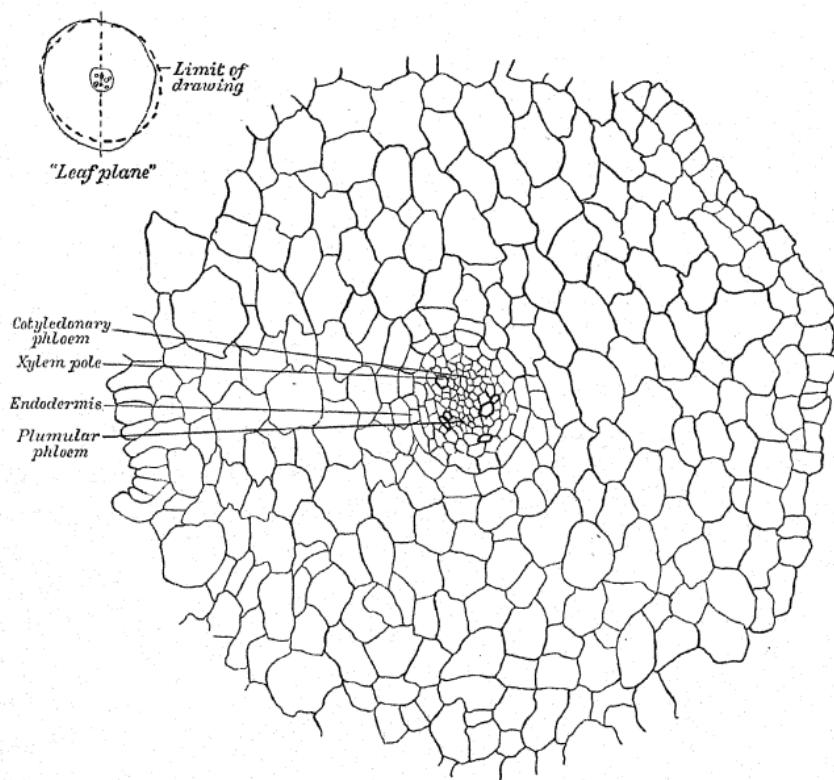
Fig. 16. T.S. of lower region of root of 4-weeks-old seedling.

Most of the food material contained in the embryo seems to have been absorbed except the oil-drops, which are still visible.

At later stages in the development of the seedling it is difficult to obtain a complete series of sections from the tip of the cotyledon to the end of the root because of the right-angled bend which the
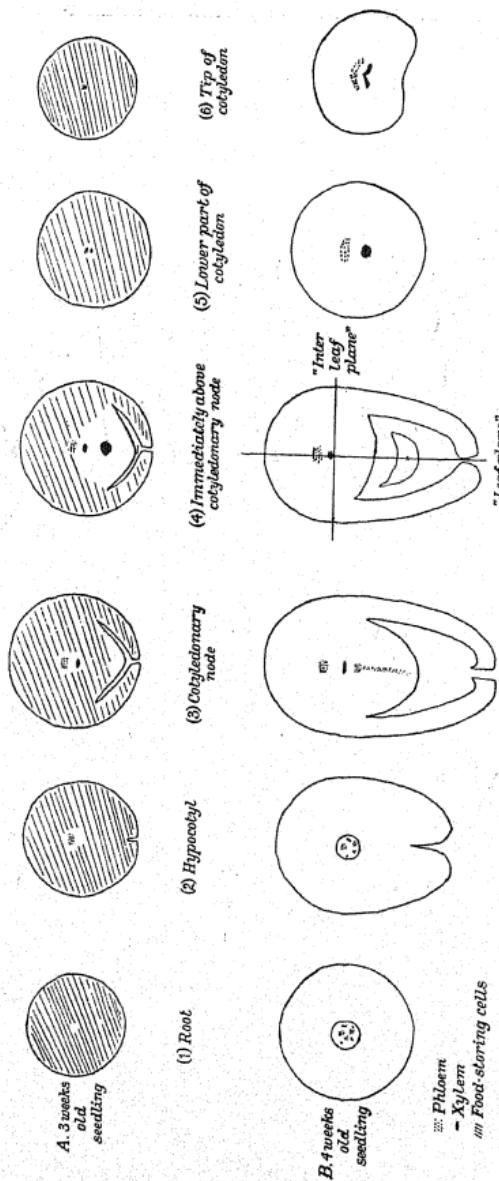
Fig. 17. Transition from root to cotyledon.

root makes with the cotyledon, thus rendering it practically impossible to obtain completely transverse sections of the cotyledonary node.

A 6-weeks'-old seedling (Fig. 9 (4)) has a very similar structure to that just described for 4 weeks except that the root is usually more definitely tetrarch or triarch (Fig. 19). A very clearly defined endodermal layer is present in the root and a slight thickening of the walls of the cells immediately within the epidermal layer is found in some cases. About three plumular leaves are present at this age, the first with one vascular strand and the others with from one to three according to age. These leaves are made up of similar small parenchymatous cells and have no stomata and no differentiation into palisade
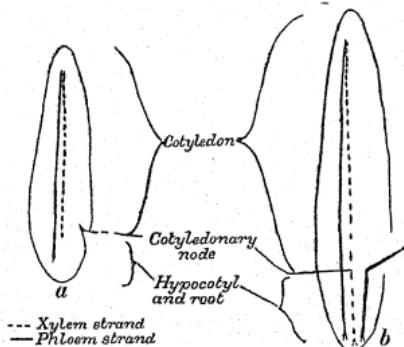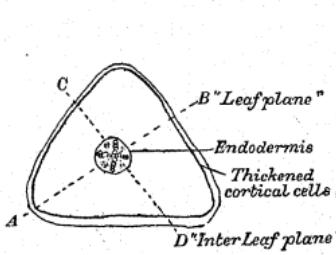
Fig. 18   Fig. 19

Fig. 18. Diagrams to show transition from cotyledon to root in L.S. through "leaf plane." (a) 3-weeks-old seedling (b) 4-weeks-old seedling.
Fig. 19. Tetrarch primary root from 6-weeks-old seedling.

and spongy mesophyll. A few cells are larger than the rest, similar to those contained in the arms of the cotyledonary sheath, and they contain groups of needle-shaped crystals.

Roots which may perhaps best be regarded as adventitious appear immediately below the cotyledonary node, i.e. in the hypocotyl, even in seedlings which are only a month old. These originate in some cases opposite the cotyledonary phloem group and sometimes opposite either of the poles of the diarch plate. In the younger stages there are usually more adventitious roots than there are plumular leaves. In older seedlings these adventitious roots grow and become similar in size and apparent importance to the primary root (Fig. 9 (6)). The primary root itself usually ceases to function and withers away when the plant is about 2 months old.

D. ANATOMY OF YOUNG PLANT DURING FIRST YEAR OF LIFE

The young pineapple plants were transferred to pots of leaf mould when about 3 months old. By this time the endosperm of the seed has been completely used up and the cotyledon has ceased to function, as shown by its shrivelled condition; the empty seed coat may remain attached for a short time, but eventually it drops off (Fig. 9 (7)). The primary root has ceased to function some time before. This young independent plant possesses about six plumular leaves and a short stem, from the base of which several adventitious roots are given off. There does not appear to be any particular relation between the number of leaves and adventitious roots. From this age until the plant is about 18 months old (which is the present age of the plants) they do not change in form but only increase in size and in the number of leaves and roots.
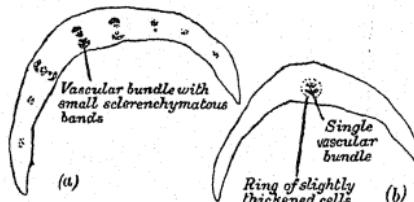
Fig. 20. Diagrammatic T.S. of first plumular leaves. (a) 2nd plumular leaf.
(b) 1st plumular leaf.
Fig. 21. Raphides from leaf cell.
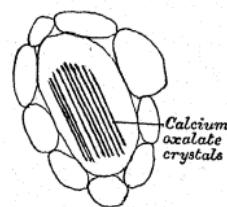
Leaf structure.

The structure of the first plumular leaf is to some extent like that of the cotyledon. Its shape is different, for, instead of being a cylindrical absorbing organ remaining undergound, it is a flat assimilating structure. The resemblance lies in the fact that both possess a single central collateral vascular bundle while all the later leaves develop a number of vascular strands without any prominent central bundle (Fig. 20).

The single bundle of the first leaf is surrounded by a ring of cells which are slightly thickened (Fig. 13). Neither the first nor the other young leaves of a seedling 6 weeks old, as stated on page 215, possess any lignified vascular elements, but the vascular bundles are in-

dicated by small groups of cells (pro-cambial strands), about three to six in number in the second and third plumular leaves but only *one* in the first leaf. The mesophyll tissue of the leaves is composed of small cells containing chloroplasts, with the exception of a few larger cells here and there which contain raphides of crystals like those found in the arms of the cotyledonary sheath (Fig. 21). These crystals are insoluble in acetic acid but they dissolve, though very slowly, in concentrated hydrochloric acid and nitric acid, showing that they are very probably calcium oxalate crystals.

A change occurs in the structure of the leaf before the plant is 3 months old. By this time the first plumular leaf has nearly withered away and the outer, i.e. the older, leaves now possess a number of vascular strands, sometimes as many as eleven. There is no definite midrib to the leaf, the bundles being very similar in size, though those
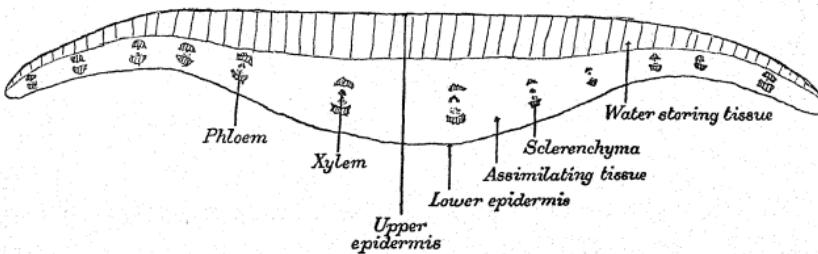
Fig. 22. Diagram of leaf structure.

towards the margins are usually somewhat smaller than the rest, and they are distributed at approximately equal intervals along the blade. Each bundle consists quite normally of a group of phloem and a few xylem elements, the xylem being placed towards the inner upper surface of the lamina, the protoxylem being nearest that face. Above and below the larger bundles the cells show slight thickenings of their walls, foreshadowing the future groups of sclerenchyma. There is also some differentiation in the ground tissue of the leaf: the cells towards the upper surface of the leaf are larger than those nearest the lower surface and they possess no chloroplasts. This differentiation of the ground tissue of the leaf becomes more distinct as the plant gets older. The cells of the tissue towards the upper surface become very much larger than those of the lower and there are usually about two rows of cells in the upper region while the tissue towards the lower surface is composed of five or six layers (Figs.

22 and 23). Both types of cell are rounded at first, but by ... .e
the plant is about a year old the cells towards the upper su... ace
have become elongated in a direction at right angles to the epidermis,
after the manner of palisade cells in an ordinary leaf. There is how-
ever no differentiation into palisade and spongy parenchyma, these
two upper cell layers being totally devoid of chloroplasts and
apparently having a water-storing function. If a leaf or section of
a leaf is left exposed to the air, or immersed in a rather strong plas-
molysing solution, these water-storing cells lose some of their water
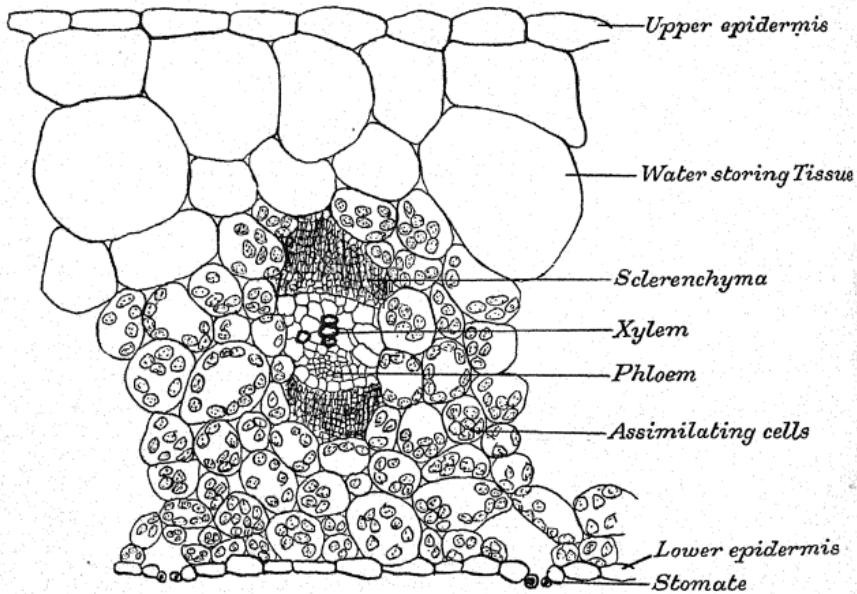
Fig. 23. Part of T.S. of leaf of 4-months-old plant.

and partially collapse, so that the walls at right angles to the surface
are thrown into folds (Fig. 24).

The older leaves are also characterised by the considerable
development of sclerenchymatous fibres which occurs in connection
with the vascular bundles. A group of fibres usually develops above
and below the vascular bundle in the well-known "girder" fashion,
the largest group being as a rule on the phloem side of the bundle.
Very often the bundles towards the margins of the leaves show a
relatively greater development of sclerenchyma and a smaller

d????ment of xylem and phloem than do the more central bundles. The xylem of the bundles consists of spiral, annular and reticulate vessels.

The upper epidermis is composed of larger cells than those of the lower epidermis and the stomata are confined entirely to the
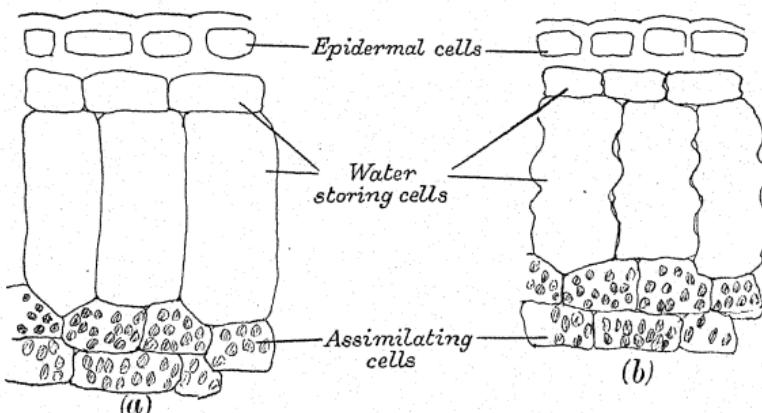
Fig. 24. Water-storing tissue of leaf in L.S. (*a*) Normal. (*b*) After losing water.
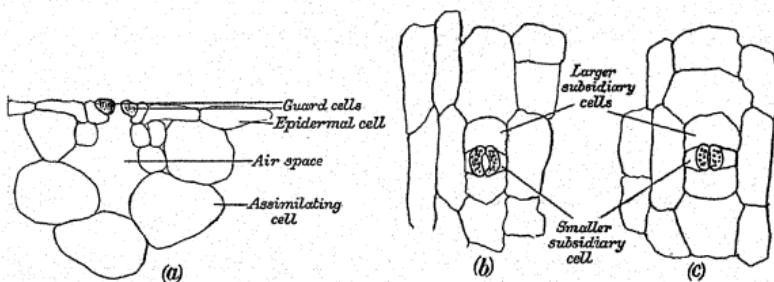
Fig. 25. Stomata from lower epidermis. (*a*) In section. (*b*) Pore open, surface view. (*c*) Pore nearly closed, surface view.

lower epidermis. The stomata are small and project slightly beyond the epidermis (Fig. 25 *a*). They lead to rather large air spaces. Seen in surface view, the stomata seem always to have four subsidiary cells, two parallel to the guard cells and two, slightly larger, at right angles. In surface view the subsidiary cells parallel to the guard cells of the stomata appear smaller than they actually are, as the

guard cells partly overlie them, particularly when fully turgid, and the extent seen is thus related to the condition of the stomatal pore (Fig. 25 *b*, *c*).

Another characteristic feature of the leaf is the production of multicellular hairs which first appear when the plant is about 4 months old. In the young plants and on the younger leaves of the older plants these hairs are quite small, and seem to be of a glandular nature. They consist at this stage of a stalk of one or two tiers of
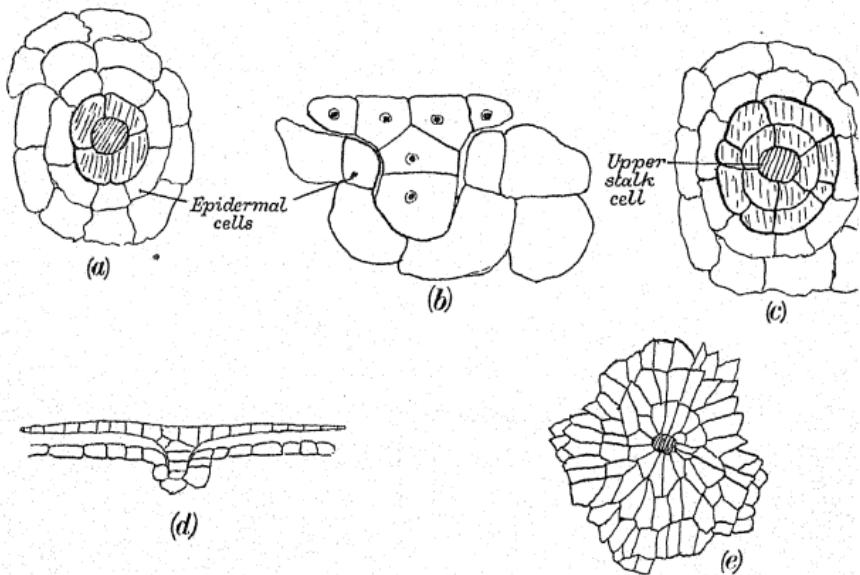
Fig. 26. Hairs from leaf. (*a*) Surface view of young glandular hair. (*b*) Section of young hair. (*c*) Surface view—from slightly older leaf. (*d*) Section of older hair. (*e*) Surface view of older hair.

one cell each and a more or less spherical head of four or five cells (Fig. 26).

These hairs appear on both surfaces of the leaf. On the older leaves they become very large by division of the cells of the head until an umbrella-shaped covering of the epidermal cells is formed (Fig. 26). Then the cells lose their contents and become dead and the hairs appear as lighter coloured spots on the dark green background of the leaf. Thus, in the older leaves from a plant aged about 1 year, these hairs are large enough and close enough together practically to cover the surface of the leaf, giving it a greyish green colour.

Root structure

The primary root, as already stated, does not function for very long but dies away about the time the seedling is 2 months old. The structure of the primary root described on p. 215 for a 6-weeks-old seedling alters mainly in the amount of thickening of the endodermis. This has already begun at 6 weeks of age, but it becomes
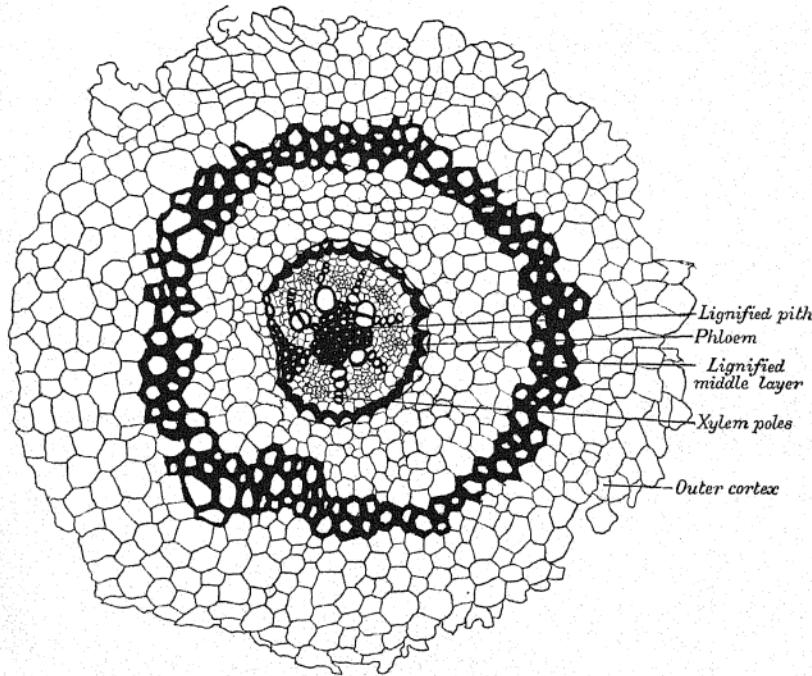
Fig. 27. T.S. of adventitious root of 4-months-old plant.

greatly intensified by the time the plant is 2 months old. The radial and inner tangential walls of the endodermal cells become very much suberised—a U-shaped band of thickening being laid down which is very conspicuous in transverse section (Fig. 27).

At this stage in development the primary root withers away and its place is taken by a number of adventitious roots. In a seedling of the age of 2 months these adventitious roots have a structure

similar to that of the primary root—i.e. they are usually tetrarch with a conspicuous endodermis and a slight thickening of the walls of the cortical cells immediately within the epidermis. At the age of 4 months the thickening of the cell wall of the various parts of the root has increased very considerably. Apparently, by division of the outer cells of the cortex, the cortical cells which were already slightly thickened in a 2-months-old seedling have now become displaced into the middle of the cortex, and have become very much more lignified. The endodermis is, if anything, still more conspicuous than before, while the pith cells in the centre of the stele have become very heavily lignified, their walls being much thicker than those of the xylem of the root poles which they connect together. The number of
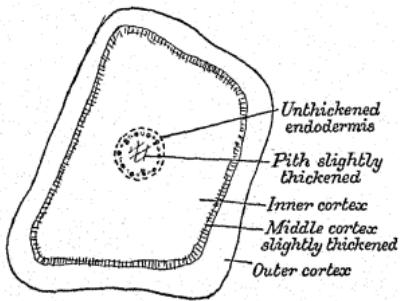
Fig. 28   Fig. 29

Fig. 28. Diagram of T.S. of short, wide root of 9-months-old plant.
Fig. 29. T.S. of upper region of stem at node of 3rd plumular leaf.

root poles in the older parts of the root has increased to six or seven, giving a hexarch or heptarch root (Fig. 27).

After this stage the character of the root does not change greatly. The lignification of the cortical cells increases somewhat and in some cases the thick-walled cells comprise more than half of the cortex, but this character varies even in different roots from the same plant. The older plants show a good deal of variation in the structure of their roots. The majority of them have a thickened endodermis and some degree of lignification in the cortex and in the pith, but very often there are some roots, usually those which are the largest in diameter, which do not show all these characters, or only to a slight degree. Sometimes both endodermal thickening and lignification of the pith is lacking. These roots, though large in diameter, are usually very short and seem to be young roots (Fig. 28).
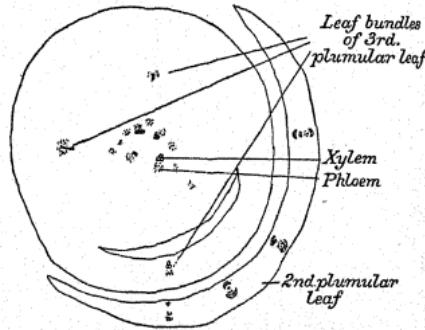
The number of xylem poles varies roughly with the diameter of the root. In the larger roots there may be as many as twelve or thirteen poles at the base of the root, i.e. in the oldest part, but towards the tip where the diameter gets much smaller this number may decrease to as few as three or four.

Stem structure

The stem at all ages is extremely short and its structure does not alter very much as it gets older. In the upper part of the stem the structure is that of a typical monocotyledon with a number of vascular bundles arranged rather irregularly. The leaf nodes are very close together and the leaf bundles, as they prepare to pass into the stem, lose the groups of sclerenchyma associated with them. The bundles pass into the stem "quickly," making almost a right-angle bend, so that in a transverse section the elements are cut longitudinally. As they reach the centre the bundles are grouped together irregularly with the xylem towards the centre of the stem and the phloem towards the outside (Fig. 29). In many cases the lignified xylem has disappeared. The rest of the stem consists of thin-walled parenchymatous cells, a few of which contain groups of crystals.

Lower down the stem the structure changes as we come to the region where the adventitious roots are given off. Adventitious roots are now formed at a level above that of the insertion of the lowest leaves, i.e. well into the epicotyledonary region. The first indication of the change of structure referred to is the recognition of a cylinder of meristematic tissue (Fig. 31 *a*) (presumably pericyclic) several cells deep within an endodermis, the character of which becomes more marked as we proceed downwards. These tissues are interrupted by the occasional exit of the adventitious roots.

The vascular tissue at this level thus differs from the leaf trace system shown above, and is condensed in a cylinder or "stele" of irregularly arranged xylem and phloem elements surrounded by pericycle and endodermis (Figs. 30 and 31).

When adventitious roots are given off a part of the xylem and phloem begins to pass out and soon arranges itself, with the xylem poles and phloem groups alternating. The root very soon develops the thickened cortex. The structure of the stem does not alter much from this point. More and more of the vascular tissue continues to pass out into adventitious roots. In a 9-months-old plant there are sometimes as many as seven or eight roots appearing in one transverse section of the stem. The central mass of xylem and phloem gets
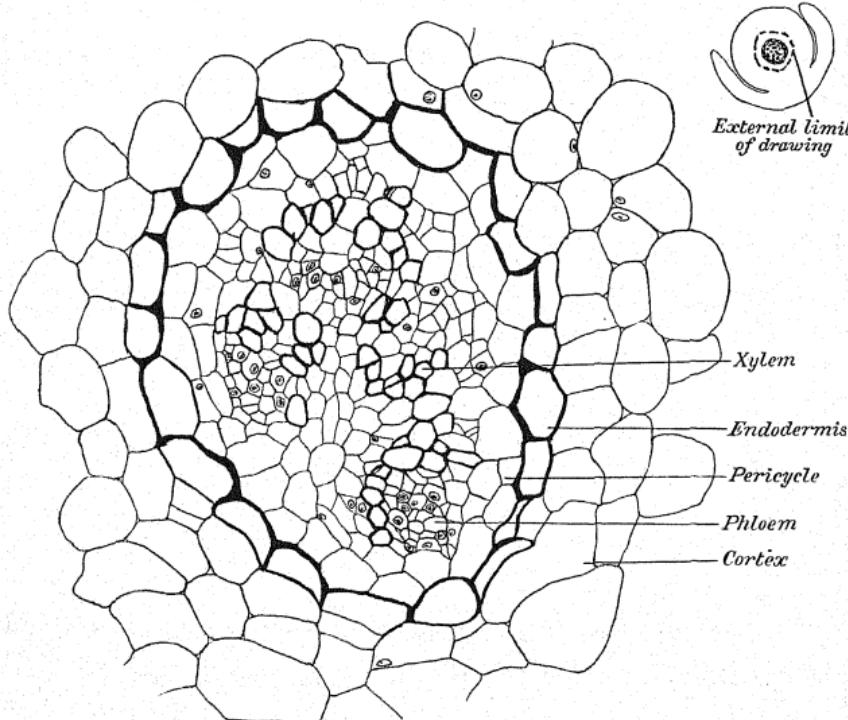
Fig. 30. T.S. of lower region of stem of 2-months-old seedling.
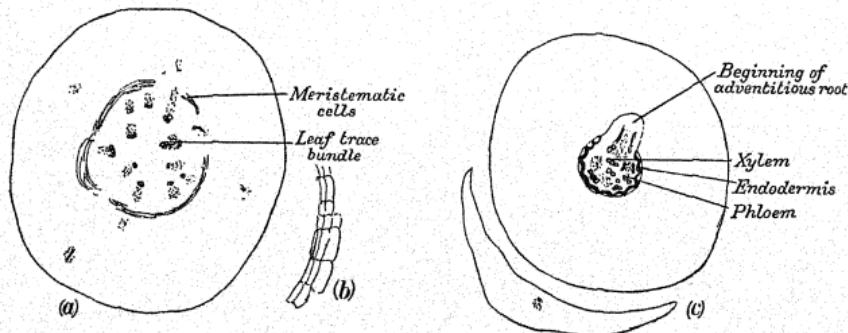
Fig. 31. Diagrammatic T.S. of lower regions of stem. (a) Region of meristematic cells. (b) Meristematic cells enlarged. (c) Region with distinct endodermis.

smaller and smaller, until finally what is left passes directly wholly into a root. The parenchymatous tissue of which the cortex of the stem was composed gradually disappears, leaving the roots free.

SUMMARY

The *seed* is small with a pointed end and one flat side, ribbed by unequal development of the middle layer of the testa. The cells of the endosperm, except the peripheral aleurone layer, contain large starch grains and small proteid granules, while the embryo itself stores oil in addition.

The *embryo* is small and obliquely placed at the pointed apex and consists almost entirely of cylindrical absorbing cotyledon. Elongation of the central cells is clearly observable in the embryo, extending from the tip to within a short distance above the plumular growing point.

Germination is of normal hypogeal type. Under favourable conditions the embryo emerges in about 3 weeks from the time of sowing. The form of the cotyledon is simple with a cylindrical distal absorbing region and proximal, asymmetrical short sheathing base. Growth starts in the cotyledon, later the cells of the radicle become active, and finally the plumule emerges from the cotyledonary sheath.

Structure of seedling at 1 month. The cotyledon has developed its short sheathing base. The plumular bud has developed one leaf which is not visible but wrapped round by the cotyledonary base. The radicle has been pushed out and has itself slightly elongated.

The cotyledon shows a single collateral strand throughout its entire length but the phloem and xylem are somewhat separated. The protoxylem of this strand is exarch. The first plumular leaf also has only one strand, which is less differentiated than that of the cotyledon. The hypocotyl and base of root show an approximation of these strands resulting in two phloem groups, the one a continuation of that of the cotyledon and the other of that of the first plumular leaf and lying in a plane passing through the centre of these members ("leaf plane") and at right angles (i.e. in a plane passing between these members, "inter-leaf plane") to a mass of xylem with two poles.

The root in its later formed part shows three to four xylem groups in its diagonal planes and an equal number of alternating phloem groups.

At 3 weeks there is no vascular structure in the plumular position, and that in the cotyledonary position is only discernible below the cotyledonary node for a short distance.

Young plant. The independent adult form is established at about 3 months, by which time the seed store is used up in the cotyledon and the primary root shed, and even the first leaf is withering. Plumular leaves and adventitious roots are continually being added. The former show numerous vascular strands supported by sclerenchyma, no midrib, a water-storing hypoderm on the upper surface and an elaborate covering of peltate hairs on both surfaces. The adventitious roots may have numerous xylem poles apparently correlated with the diameter, and generally develop a sclerotic middle cortex and a sclerised pith as well as a much thickened endodermis. In certain short roots of large diameter these may be missing.

Both the epicotyledonary and the hypocotyledonary axes are very short. The plumular axis develops at about the level of the insertion of the second leaf, a curious cylinder of meristematic cells in the region of the pericycle consisting of several cell layers. Immediately below and to the outside of this cylinder a well-developed endodermis is found. This constitutes a distinct "stelar" structure.

THE

NEW PHYTOLOGIST

THE ARBORESCENT HABIT IN ANGIOSPERMS

A REVIEW

(Continued)

BY H. BANCROFT

CONTENTS

V. EVIDENCE FROM THE STRUCTURE OF THE ANGIOSPERMS

(1) Seedling anatomy

MUCH attention has been given, both in this country and in France, to seedling anatomy, one of the chief aims of the researches being phylogenetic. While "there is a remarkable uniformity in the main features of seedling anatomy, particularly as displayed in the hypocotyledonary region[1]," phylogenetic conclusions appear at present to be somewhat conflicting. Diversity of opinion centres round three points:

(1) Whether seedling anatomy may be used profitably in deducing the phylogeny of the Angiosperms[2].

(2) Which type of seedling root structure, diarch or tetrarch, is

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[1] Thomas(172), p. 448. See also Sinnott(148), whose seedling studies lead him to regard the cotyledonary node as being very uniform in structure throughout large groups.

[2] Cf. the negative views of de Fraine(45), Hill and de Fraine(75, 76), Lee(102) and Smith(156), with those expressed by Arber(2), Compton(40), Fritsch(51), Sargant(129, 130), Tansley and Thomas(165, 166), and Thomas (168, 169).

the more primitive[1]. These two questions, of course, lead up to the main question under consideration here, namely,

(3) What may be the primitive habit of the Angiosperms as deduced from seedling structure[2].

Professor Compton, in his comprehensive researches on the seedling anatomy of the Leguminosae, points out that: "From the standpoint of phylogeny, as well as that of the better comprehension of anatomy, it is clearly important to determine, with as much precision as possible, what relations exist between the seedling structure, and the size, form, habit and general morphology of the species" ((40), p. 3).

A brief survey of the main ascertained facts of seedling habit and anatomy, and a correlation of these facts with the mature habit of the various species must therefore be made, in order to determine whether the points of discussion mentioned above may be decided on our present knowledge of seedlings and their structure[3].

[1] Opinions in favour of the primitiveness of diarchy are given by Hill (*New Phytol.* Report of the Discussion at York, 1906), Hill and de Fraine (76), Lee (101, 102), and Tansley and Thomas (165); and of tetrarchy by Arber (2), Compton (40), Sargant (129, 130), Tansley and Thomas (166), and Thomas (168, 169).

[2] Cf. the views of Compton (40) and Thomas (168, 169), who incline to the belief that the arborescent type is the more primitive in Angiosperms, with those of Sargant (130), who considers that the herbaceous type is more likely to be primitive, on account of its greater plasticity.

[3] It may be well to give here a résumé of the chief features of seedling anatomy in general. According to the extended researches of Dr Miles Thomas ((168, 169, 170, 171); see also (172), where the results of earlier papers are summarised), it appears that the variations in seedling anatomy are not due to difference in basal plan, but to the varying behaviour of a common fundamental unit of vascular structure and its associated strands. This fundamental unit is the cotyledonary midrib, which is essentially a "double bundle" or "triad," resolving itself, while still actually in the cotyledon, into two groups of phloem with a single protoxylem strand placed between them; associated with this double bundle there are lateral cotyledonary strands of collateral organisation, and the variations in hypocotyl structure are due, in great measure, to "linkage, fusion or independence" of the components of this cotyledonary vascular system, and to their relative position and state of development (Holden and Clarke (82), p. 335). The stage at which plumular development takes place affects the manner in which the epicotyledonary strands exert their influence upon the cotyledonary vascular system at the cotyledonary node; and this, also, is productive of variations in the hypocotyl structure. For example, in hypogeal types with plumular development relatively advanced at an early stage, the plumule traces may remain independent of the cotyledonary strands (Compton (40), pp. 101, 104; see *Cesalpinia sepiaria*, p. 21, Pl. 3, Figs. 53, 54; also the hypogeal climbing Vicieae, p. 107: Davey (43), p. 576; see *Juglans nigra*, pp. 583, 584, Figs. 6, 7). In other cases, the epicotyledonary strands may sooner or later enter into relations with the lateral cotyledonary strands (Compton (40), p. 104).

It should be noted that difference in number and constitution of the cotyledonary strands may occur in species "which show identical hypocotyl

structure, so that the number of cotyledon strands in no sense 'controls' the number of groups in the hypocotyl" (Thomas(172), p. 448); nor does the type of vascular arrangement found in the hypocotyl necessarily determine the number of root poles (Holden and Bexon(80), p. 591; Thomas(169), p. 713, Text-fig. 25; cf. 1 and 2, 3 and 4). But it is from the different *behaviour* of these various vascular strands in the cotyledon and hypocotyl that certain types of root structure result, at varying levels below the cotyledonary node; these types are referable either to the "Cruciform" plan, or to the "Diagonal" plan (Thomas(169), p. 698).

According to present knowledge of seedling structure, the cruciform plan is much the more common. Of this plan, there are two main types: the tetrarch type, with four root poles, two in the cotyledonary plane, and two in the inter-cotyledonary plane; and the diarch type, where only two—the cotyledonary—poles are present (Thomas(169), p. 713, Text-fig. 25, 1–5; p. 730, Text-fig. 42; p. 731, Text-fig. 43).

The comparatively rare diagonal plan is characterised by the fact that there are root poles lying *between* the cotyledonary and the intercotyledonary planes. The types included under this general plan are: diagonal tetrarchy; hexarchy, with the four diagonal root poles *plus* the two cotyledonary poles; octarchy, with the four diagonal poles *plus* the two cotyledonary and the two inter-cotyledonary poles; and double-diagonal octarchy, in which the eight root poles occur in pairs in the diagonal planes (Davey(43), p. 578, Fig. 1; Thomas(169), p. 713, Text-fig. 25, 6; and p. 727, Text-fig. 41, 1–2).

In all these cases, there is an even number of root poles; an odd number may, however, result from an asymmetrical behaviour of the vascular strands, as, for example, in *Tilia vulgaris* (Holden and Clarke(82)). In this species, normally, the lateral cotyledonary strands become linked with the central strand or triad, and then separate from it again, so that six strands, three from each cotyledon, occur in the hypocotyl; the triads of the two cotyledons form the two cotyledonary root poles, and the lateral strands fuse in pairs, one from each cotyledon, to form the intercotyledonary poles, cruciform tetrarchy thus resulting in the root. Triarchy may, however, occur in *Tilia vulgaris* when the lateral cotyledonary strands on *one* side of the seedling *remain fused* with the midrib, so that only four strands enter the hypocotyl; the "compound" midrib strands form the two cotyledonary poles, and the two "free" laterals fuse to form a third pole. In the same species, pentarchy may result from asymmetry of a reverse type; the lateral cotyledonary strands, having become free from the midrib, as in normal cases, may *remain free* on *one* side of the seedling, while the other two laterals fuse in the ordinary way, so that five root poles are produced.

Tilia vulgaris thus shows the production of an odd number of root poles in a case where plumular influence does not affect the number of strands in the hypocotyl. In some cases, however, an odd number of root poles may result where plumular traces are continued into hypocotyl and root independently; as, for example, in the hypogeal climbing Vicieae, where two of the root poles are formed by the cotyledonary strands, and a third is plumular in origin (Compton(40), p. 107).

While the vascular system of dicotyledonous seedlings in general is comparatively stereotyped, that of monocotyledonous seedlings shows great variety. It has been shown, however, that the triad or double bundle lying in a median position in each cotyledon of Dicotyledons has its equivalent in the twin strands in the single cotyledon of Monocotyledons, the twin strands having been derived by the disappearance of the central protoxylem of the triad, and the production of metaxylem, collateral with the phloem groups of the triad (see Arber(3), p. 172; Thomas(172)). Further, Miss Sargant(129) has brought forward evidence to indicate that the variations in vascular anatomy of mono-cotyledonous seedlings may be referable to a tetrarch plan. Variations resulting in polyarchy are due partly to the characteristically broad sheathing

The arrangement of the orders and families reviewed in this section follows Engler's System (49), and reference has been made, where necessary, to the work of Lubbock (107), for seedling habit.

Dicotyledons

Verticillatae.

Miss Davey has found that in four species of *Casuarina*, a genus of specialised woody xerophytes, the seedlings are slender and wiry with a relatively long hypocotyl and epigeal germination; root structure is of the typical cruciform tetrarch plan ((43), pp. 579, 580).

Piperales.

In this order, which contains herbs, shrubs and shrubby climbers, the typically epigeal seedlings appear to be characterised by a uniformly diarch root symmetry (T. G. Hill (66, 67), A. W. Hill (65), Chauveaud (35)).

Salicales.

Of this order of woody plants, two species of *Salix*, *S. Caprea* and *S. repens*, have been examined by Miss Davey ((43), p. 580); both possess very small epigeal seedlings and diarch root symmetry. It should be noted that, while *S. Caprea* is definitely arborescent, *S. repens* is a much smaller, though still woody, type of rather variable habit.

Myricales.

Two species of the shrubby genus *Myrica* were found to possess small and wiry seedlings with epigeal cotyledons. The stele of the hypocotyl near the cotyledonary node shows diarch root structure, while that of the root is of the cruciform tetrarch plan ((43), pp. 580–582).

Juglandales.

The arborescent Juglandaceae comprise both hypogeal and epigeal forms. The four species of *Juglans* so far examined have large seeds and seedlings with a short, thick hypocotyl, early plumular development and considerable uniformity in the structure of the hypocotyl. Cruciform tetrarchy occurs in the root stele. The seeds and seedlings of *Carya* are similar to those of *Juglans* in habit and

base of the single cotyledon, which may introduce minor lateral bundles into the hypocotyledonary system; they may also be caused by the internodal abbreviation of the plumule, and the direct, independent passage of plumular traces into the root.

germination, but are smaller; the root structure of *C. olivaeformis* is octarch, and that of *C. amara* hexarch, both forms thus showing a combination of the diagonal and cruciform plans of symmetry. *Pterocarya rhoifolia* has epigeal cotyledons, a long hypocotyl, fairly robust seedling habit, and cruciform tetrarchy of the root stele; and *Fortunea chinensis*, with its smaller seedlings, shows a similar structure and behaviour in germination ((43), pp. 583–587).

Fagales.

The seedlings of the Betulaceae are typically small, with long slender hypocotyls and epigeal cotyledons. In these slender types, root structure is diarch (*Alnus incana* and *A. glutinosa*, *Betula excelsa* and *B. pumila*); diagonal tetrarch (*Alnus cordifolia*); or cruciform tetrarch (in *Carpinus Betulus* and *C. Ostrya*, which have somewhat larger seedlings than the preceding types). *Corylus avellana* possesses a large seedling with fleshy hypogeal cotyledons and early plumular development; the root stele is of the cruciform tetrarch type.

The members of the Fagaceae have typically very robust seedlings, with large, thick, hypogeal cotyledons, as in *Quercus* and *Castanea*; *Fagus*, however, has seedlings with an erect, comparatively slender hypocotyl and broadly expanded, epigeal cotyledons. In the types of which the seedling structure is known, the species of *Quercus* show hexarch root steles with occasional individual variations (e.g. diagonal tetrarchy in one seedling of *Q. Robur*; double-diagonal octarchy and heptarchy in some specimens of *Q. Ilex*). The large robust seedlings of *Castanea sativa* also are hexarch in their root symmetry; while *Fagus sylvatica* shows, apparently, the very constant development of double-diagonal octarchy in the root ((43), pp. 587–595).

The mature habit of members of the Fagales is exclusively woody; and their seedlings are therefore of considerable interest, since they show great diversity of size and habit, and also a wide range of root structure from diarchy (cruciform plan) to double-diagonal octarchy, while there are in addition cases indicating a transition from one type of symmetry to another ((43), p. 594).

Urticales.

The seedlings of members of this order, so far as examined ((43), p. 595; (35), p. 295), are very uniform in their epigeal habit, and in their diarch root symmetry, though they differ considerably in size; the mature habit of the different types studied is also variable,

being arborescent (*Celtis australis* and *C. occidentalis*, of the Ulmaceae; *Morus alba* and *Maclura aurantica*, of the Moraceae); herbaceous (*Urtica dioica* and *U. cannabina*, and *Parietaria officinalis*, of the Urticaceae); and a herbaceous climber (*Humulus Lupulus*, of the Moraceae). It should be especially noted that there is considerable similarity of habit and structure between the seedlings of *Urtica cannabina* and *Morus alba* ((43), p. 595).

Polygonales.

The one family of this order, the Polygonaceae, contains chiefly herbs of varying size; the seedlings also vary in size, and diarchy and tetrarchy are both represented (Thomas (168), p. 85).

Centrospermae.

In this order, composed largely of herbs and undershrubs, the largest seedlings are to be found in the Nyctaginaceae, and it is in these seedlings that a cruciform tetrarch structure occurs in the hypocotyl and, in some cases, also in the root; in other cases, the root stele is diarch, after a tetrarch stage in the hypocotyl. Diarchy characterises the smaller and simpler seedlings of all the other families of the order, so far as they have been investigated[1].

Ranales.

This order includes plants of various habit, from small herbs to trees of considerable size. The seedlings of more than fifty species of the Ranunculaceae have been examined[2], ranging from that of the minute annual herb *Myosurus minimus*, to those of the larger herbs *Delphinium* and *Paeonia*, and the shrubbery climbers of the genus *Clematis*. The seedlings vary in size and in slenderness of habit, but agree generally in the possession of epigeal cotyledons, exceptions including some species of *Paeonia* and *Clematis recta*, where they are fleshy, and do not escape from the seed. Root-like structure is typically found at a high level in the hypocotyl, and the structure of the root itself is uniformly diarch; in two species of *Clematis* a tetrarch stage is temporarily present in the hypocotyl.

Decaisnea Fargesii, a woody type belonging to the Lardizabalaceae, has been found to possess a robust seedling, with a long hypocotyl, epigeal cotyledons, and diarch root structure (Thomas (169), p. 709).

Of the Berberidaceae, the genus *Berberis*, comprising shrubby

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[1] Hill (68), Hill and de Fraine (74); see also Thomas (169), p. 729, where it is noted that only about 6 per cent. of the Centrospermae show tetrarchy.
[2] Thomas (169), pp. 701–708; see also Chauveaud (35), Gérard (56), Sargant (129), Sterckx (159), Tansley and Thomas (165).

types, shows both diarch and tetrarch root structure; the seedlings vary somewhat in size, but are comparatively slender, with epigeal cotyledons. A point of interest is that the small seedling of *B. Lycium* has a tetrarch root, while the larger seedling of *B. aristata* may show a reduction to triarchy; further, tetrarchy and diarchy both occur in *B. macrophyllum* ((169), pp. 708, 709).

In the Magnoliaceae, a family of shrubby and arborescent forms, the seedlings figured by Dr Thomas are robust with epigeal cotyledons. Three species of *Magnolia* show tetrarchy, and one species diarchy of the root stele. *Liriodendron tulipifera* shows a tetrarch stage in the hypocotyl, while the root itself is diarch ((169), pp. 709, 710).

The species of the Calycanthaceae (shrubs) are characterised generally, so far as they are known, by the possession of diagonal tetrarch root symmetry ((169), p. 711).

Two species of *Anona* (Anonaceae, a family of woody forms) show diarchy of the root stele; and the Lauraceae, also woody, show tetrarchy ((169), pp. 711, 712).

Thus, while the herbaceous Ranunculaceae have uniformly diarch root steles, the more woody families of the Ranales exhibit considerable variation in structure, cruciform tetrarchy being frequent. A very significant feature of the order is the almost invariable presence, at an early stage of epicotyl development, of a cambium connecting the vascular strands; this occurs even in the herbaceous Ranunculaceae, where cambium is absent at a later stage (Blackburn(23), p. 179). In certain cases amongst the Ranunculaceae, cambium has been recorded not only in the epicotyl, but also in the hypocotyl, of young seedlings. In *Eranthis hiemalis*, for example, primary strands of epicotyledonary origin are continued downwards into the hypocotyledonary tuber, where they are connected by a cambium ((23), p. 154); and in *Paeonia herbacea*, the tuberous development of the hypocotyledonary node and the hypocotyl is largely due to rapid growth of the cambium ((23), p. 162); these forms are, however, somewhat specialised, being of geophytic habit.

The very general occurrence of a normal active cambium at the seedling stage of Ranalean types, even where it is absent in the adult plant, suggests the primitiveness of cambial growth and of woody structure for the whole order, an interesting point in view of the fact that, on grounds of floral structure, the Ranales, as a whole, have been considered as basal amongst Angiosperms[1].

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[1] Arber and Parkin (8, 9); Wernham(185). Cf. however the view of Hutchinson ((87), and (88), pp. 4, 5) that the Ranales (in the generally accepted

Rhoeadales.

This order consists mainly of herbaceous forms, though shrubby types are general in the Capparidaceae; the seedlings vary in size, but are epigeal in their mode of germination. Members of the Cruciferae, Papaveraceae, Resedaceae and Capparidaceae have been examined, and considerable constancy of structure is revealed, diarch root steles characterising the group. It should be noted that two species of *Cleome*, belonging to the typically shrubby family Capparidaceae, show indications of tetrarchy in the hypocotyl ((169), pp. 714–720; (35); (165)).

Rosales.

A large number of members of this order have now been investigated, and considerable variety of seedling root structure has been discovered; there is, of course, a wide range of mature habit exhibited, not only in the order as a whole, but also in individual families, e.g. the Rosaceae and the Leguminosae.

The Crassulaceae, a family of succulent herbs and undershrubs having fleshy seedlings, show diarchy of the root and hypocotyl, so far as known ((169), p. 724).

Of the Saxifragaceae, *Saxifraga muscoides*, *S. Aizoon*, *Heuchera alba* and *Philadelphus grandiflorus* have been examined; their epigeal seedlings are all very slender and have diarch structure in the root and hypocotyl, although there is considerable range in the mature habit of the species, *S. muscoides* being a small alpine herb, and *Philadelphus* a shrub ((169), p. 724).

Those members of the two woody families, Pittosporaceae and Hamamelidaceae, which have been examined showed certain individual peculiarities, making it difficult to decide to which type the root structure should be referred ((160), pp. 725, 726).

The arborescent forms, *Platanus occidentalis* and *P. orientalis* (Platanaceae), have very slender epigeal seedlings with diarch root structure, though a suggestion of tetrarchy is given in the hypocotyl by the presence of four phloem groups ((169), pp. 725, 726).

The members of the Rosaceae show a wide range of structure, diarchy prevailing in the Spiraeoideae and Rosoideae (groups in which the seedlings vary considerably in size, and in which the mature habit is also variable), and cruciform tetrarchy in the woody Prunoideae; while the Pomoideae show diarchy (*Cotoneaster affinis* and *Crataegus*

sense) should be divided into two groups showing parallel floral development: the Ranales (in a restricted sense), representing a primitively herbaceous stock; and the Magnoliales, representing primitively woody types.

Oxyacantha), cruciform tetrarchy (*Pyrus Aria, P. Malus* and *P. communis*), hexarchy (*P. communis*), and heptarchy (one individual of *P. communis*), the two latter types being combinations of the cruciform and diagonal plans of symmetry. The variations in the single species *P. communis* are of interest, for in this case, at least, there is no obvious relation between seedling habit and seedling root structure ((169), pp. 721–724).

Seedling habit and anatomy as correlated with mature habit are very comprehensively known in the Leguminosae, from the work of Professor Compton[1]. The characteristic seedling root structure in the family is cruciform tetrarchy, this being very constant in certain groups, as, for example, in the woody sub-families Mimosoideae and Cesalpinioideae, and in the tribe Phaseoleae (sub-family Papilionatae), which includes herbs, shrubs and trees; in all these tetrarch types the seedlings are characteristically large. The tribe Genisteae, on the other hand, consistently shows diarchy of the seedling root stele, although the seedlings vary greatly in size. The mature habit of members of this tribe is also variable, though on the whole woody; the variation in size of the seedling, however, is not correlated with the variation in size of the mature plant. In the hypogeal Vicieae (Papilionatae), triarchy occurs throughout in connection with rapid plumular development, one of the root poles being plumular. In the Leguminosae as a whole, Compton's work indicates a broad correlation between robust seedlings and cruciform tetrarchy on the one hand, and between the tree habit and the production of large seeds and seedlings on the other; with reduction in the size of the seedlings, there may be traced a corresponding reduction in the number of root poles, resulting ultimately in diarchy.

Geraniales.

Few types of this order have as yet been investigated, the seedling structure of the shrubby genus *Ricinus* (Euphorbiaceae) being the best known (Thomas(170)). The large robust seedling has, typically, a tetrarch root, though variations have been noted in *R. communis* (Chick(36)); and it is stated that the tetrarch type of root symmetry is characteristic for the family (Thomas(168), p. 85).

Sapindales.

Cruciform tetrarch root symmetry, a slender epigeal seedling, and arborescent habit of the mature plant are combined in *Acer*

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[1] (40); note particularly the tables given on pp. 68–74. See also Holden and Chesters(81); Thomas(169), p. 726; and Gehlen(55).

Pseudoplatanus (Aceraceae) (Holden and Bexon[80]; also [168], p. 85). This type is interesting in that it shows a lateral concentration of the vascular strands in the cotyledons, the two phloem and metaxylem groups of the double bundle in each case being detached from the protoxylem and fused with their adjacent lateral strands; four diagonally placed collateral bundles thus enter the hypocotyl, as in *Calycanthus* of the Ranales; but the subsequent behaviour of the bundles leads to cruciform tetrarchy of the root stele in *Acer*, instead of to diagonal tetrarchy as in *Calycanthus* ([80], pp. 591, 592).

Impatiens Roylei (Balsaminaceae), an annual herb, possesses a fairly robust seedling with a long hypocotyl, and tetrarch symmetry of the hypocotyl and root (Holden[78]); the family is said to be characterised by tetrarchy ([168], p. 85).

Malvales.

Of the Tiliaceae, *Tilia vulgaris* has been investigated by Dr Holden and Mr Clarke[82]. The seedling is very slender although the mature habit of the species is so markedly arborescent; and the root stele is typically cruciform tetrarch. Plumular development is slow, and the epicotyledonary strands have little effect on the structure of the hypocotyl; triarchy and pentarchy may, however, result from asymmetrical behaviour of the lateral strands of the cotyledonary vascular supply[1].

Althaea rosea (Malvaceae) has been extensively investigated by Miss Bexon[22]; this large herbaceous type exhibits considerable variation in root symmetry from tetrarchy to hexarchy, comparable to that shown by the woody type, *Pyrus communis* (cf. Thomas[109], p. 724).

Parietales.

In this order, the seedling structure of the Guttiferae has been examined by M. Brandza[28], who finds that the more slender and normal seedlings of the Hypericoid sub-family—the members of which are typically herbaceous—have diarch symmetry of the root and hypocotyl; the more robust and often tuberous seedlings of the other sub-families, which contain trees and shrubs, are triarch so far as their root steles are concerned, while their hypocotyls show considerable variation in the amount of vascular tissue according to their size.

Opuntiales.

The single family, Cactaceae, is represented by extreme xerophytes with succulent stems and reduced transpiring surface.

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[1] See footnote, p. 229; cf. triarchy in the Vicieae (Leguminosae).

Pereskia is the least modified type, having large expanded, though fleshy, green leaves; its seedlings, also, are the least modified, while those of the highly specialised Mammillarias are correspondingly modified and tuberous. The seedlings of *Pereskia* and others of the more normal habit (*Opuntia* and *Nopalea*) have tetrarch root steles; while the comparatively small but modified seedlings of *Echinocereus*, *Echinopsis* and *Mammillaria*, with their swollen hypocotyls and slender roots, show diarchy[1]. The extreme specialisation of the mature habit, and even of the seedling habit, in this family demands caution in considering the results of anatomical studies.

Umbelliflorae.

This order contains both herbs and woody plants, the seedlings being of varying size; they are said to be characterised generally by diarch root symmetry (Thomas(168), p. 85).

Ebenales.

The arborescent and woody plants of this order have fairly large seedlings with a considerable variety of root structure (Thomas(171)). The Sapotaceae are characterised by diagonal tetrarchy ((171); and Smith(156)), which also occurs in species of *Diospyros* (Ebenaceae) ((171); and Wright(197)). Cruciform tetrarchy and diarchy have also been found in the Ebenaceae and Styracaceae.

Tubiflorae.

The seedling structure of a large number of members of this order has been investigated (Lee(101)); and it appears that in the Polemoniaceae, Hydrophyllaceae, Boraginaceae, Labiatae, Solanaceae, Scrophulariaceae and Acanthaceae, characteristically herbaceous families, a diarch root stele is produced; this is the case also in some members of the woody family Bignoniaceae. Tetrarchy occurs in the Convolvulaceae and in *Incarvillea Delayvei* and other members of the Bignoniaceae. In the Tubiflorae, the roots of the smaller seedlings are generally diarch, and those of the larger ones tetrarch, these latter forms comprising about 11 per cent. of the total number investigated ((101), p. 745; Thomas(169), p. 729).

Cucurbitales.

The members of this order are chiefly annual climbing herbs of rapid growth. The seedlings are of various sizes, but are generally large; they are said to be characterised by tetrarchy ((168), p. 85).

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[1] de Fraine(45); cf. the case of the Guttiferae, where the more normal seedlings have diarch roots, and the swollen types show the larger number of root poles.

Campanulatae.

About fifty species of the Compositae have been examined by Lee (102), who found that, while all the seedlings have diarch or tetrarch roots, so far as known, variations occur in nearly related species, and even in different individuals of the same species. In his diagram, drawn to scale, Lee shows clearly that in this group, at least, there is no close correlation between size of seedling and root anatomy ((102), p. 327, fig. 2; pp. 325, 326).

Monocotyledons

The seedlings of the Monocotyledons show a remarkable variety of structure as contrasted with dicotyledonous seedlings, which are characterised by comparative uniformity of vascular symmetry (Sargant (129); Arber (3), pp. 170 *et seq.*). Although the Monocotyledons are, as a group, typically non-woody, the mature habit varies greatly from that of small herbs (e.g. *Scilla autumnalis*) to that of large fleshy herbs, such as those of the Scitamineae; climbers, such as *Tamus* and *Smilax*, and arborescent forms, like the Palms, Yuccas and *Dracaena*, are also represented. The seedlings, moreover, are very varied in habit and size, though the hypocotyl is generally short, and the primary root and cotyledon are typically short-lived. The vascular structure of the root and hypocotyl may be determined by cotyledonary traces only, as in certain members of the Liliaceae, where plumular development is late; the primary root in such cases tends to be diarch or tetrarch. In cases, on the other hand, where plumular development is early, the structure of the root and hypocotyl is determined by both cotyledonary and plumular traces, and the primary root is often polyarch (see footnote, p. 229). The variation in the stage at which plumular development takes place corresponds to variation in the habit of the species; such development is early in the case of climbers and, more particularly, in that of arborescent species, with their large seedlings and somewhat persistent primary roots; and it is consequently in these cases (e.g. the Palms and *Dracaena*) where the primary root tends to be polyarch; there may be as many as eighteen xylem poles in the root of *Dracaena Draco*.

Gymnosperms

In view of the fact that the Gymnosperms are typically arborescent, or at least woody, in mature habit, mention should be made of their seedling structure by way of comparison with that of the Angiosperms. The seedling habit of the Gymnosperms varies greatly from the robust forms of the Cycads and *Ginkgo* to the slender forms

of many of the Coniferae. In the Cycads, the root stele is regarded by Dr Thomas as being typically tetrarch, though many variations occur; for example, in *Cycas siamensis* there is a tetrarch stage in the hypocotyl while the root itself is diarch[1]. *Ginkgo* also shows variation from tetrarchy to diarchy ((108), p. 83; (72)). The seedling roots of the Taxaceae and Pinaceae are typically diarch ((108), p. 84; Hill and de Fraine(70,71); Chauveaud(34)), though the Araucarians show tetrarchy and even hexarchy in the hypocotyl ((108); (70), 71; Shaw (144)); and many variations occur in connection with poly-cotyledony in the Abietineae ((70), p. 711; (71), pp. 226, 227). All specimens of the specialised members of the Gnetales which have been examined have diarch seedling roots (Hill and de Fraine(73)). This latter type of root symmetry is, therefore, most common amongst the Gymnosperms (Hill and de Fraine(69)); and it is not entirely correlated with seedling habit for, as Dr Thomas points out, the seedling anatomy of *Ginkgo*, *Torreya* and *Araucaria* is generally coniferous in type, while the habit is cycadean ((168), p. 84).

The distribution of the various types of seedling root symmetry having been reviewed, and the types correlated as far as possible with seedling habit and mature habit in the different groups, it is necessary to consider whether there is any consistency of association between the arborescent habit and size of seedlings on the one hand, and between size of seedlings and a particular type of root symmetry on the other. Professor Compton's researches have disclosed, in the Leguminosae, a *general* correlation between the arborescent habit and large seed-lings; but there are numerous exceptions to this correlation, some of them even occurring amongst the Leguminosae themselves. In the tribe Genisteae, for example, the seedlings of tree forms such as *Laburnum vulgare* may be slender, and in the Vicieae large seedlings occur in the case of herbaceous species like *Vicia Faba*. Apart from the Leguminosae, notable exceptions to the correlation between the tree habit and large seedlings are to be found in the Betulaceae, where the arborescent types *Alnus* and *Betula* have small and slender seedlings, while those of the less definitely arborescent *Corylus avellana* are large and fleshy. Both large (*Quercus* and *Castanea*) and more slender (*Fagus*) seedlings occur in the arborescent family Fagaceae; and, in other families, *Platanus*, *Acer* and *Tilia*, all arborescent, have slender seedlings, while those of the herbaceous

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[1] Thomas (168), p. 82; see also Hill and de Fraine (72), whose table on p. 457 shows considerable variety of root structure.

Cucurbitaceae are comparatively large. A further example of lack of correlation is furnished by the Urticales, the seedling of the herbaceous *Urtica cannabina* being similar in habit to that of the arborescent *Morus alba*.

Amongst the Monocotyledons, it will be seen that large size of the mature plant is to a great extent correlated with large size of the seedlings, as in the Palms and *Dracaena*; but these specialised "arborescent" types cannot validly be compared with the arborescent types of the Dicotyledons, with their normal secondary thickening; large size of seedlings in these Monocotyledons is fairly clearly a physiological necessity, and such specialised cases must therefore be ruled out in phylogenetic considerations.

Finally, a survey of the Gymnosperms, by way of comparison with the Angiosperms, shows a wide variation of seedling size in a typically arborescent group.

The foregoing considerations render it impossible definitely to correlate the arborescent habit with the possession of large seedlings in the Angiosperms, or in fact, in Phanerogams as a whole.

With regard to the second point, Dr Thomas remarks that there is "probably a broad correlation between habit of seedling and root anatomy, but the connexion is by no means close or universal" ((100), p. 731). Professor Compton finds a stable tetrarch root symmetry in large seedlings of the Leguminosae, while the small seedlings tend to show a reduction leading to diarchy ((40), p. 117). Hill and de Fraine contend, as a result of their observations, that the size and structure of seedlings are correlated directly, and remark that tetrarchy appears to be characteristic of large seedlings and diarchy of smaller ones ((76), p. 269). This certainly seems to be the case in the Centrospermae, where the large seedlings of the Nyctaginaceae may have tetrarch roots, while those of other families, generally smaller, have diarch roots. Hill and de Fraine also quote the case of the large seedling of *Dahlia Merckii* with its tetrarch root, comparing it with the smaller seedling of *Coreopsis tinctoria*, where the root is diarch after a tetrarch stage in the hypocotyl ((76), pp. 270, 271).

But, again, there are many exceptions to this correlation of seedling size and structure, some of them being shown by the work of Hill and de Fraine themselves; for example, both the large seedling of *Saponaria Vaccaria* and the small one of *S. cerastoides* have diarch roots(76, 74), and several other pairs of related seedlings differing considerably in size, but showing diarch root symmetry, are noted by these authors(76).

Hill and de Fraine further claim that the seedlings of the Cactaceae show tetrarchy in the case of the large types, and diarchy in that of the small ones ((76), p. 269); but it will be remembered that the "small" seedlings are much modified and have greatly swollen hypocotyls in spite of their slender roots, while the "large" seedlings are the more slender and normal types. In the case of so specialised a family, it is impossible to use the given data in a comparison of this kind; for Hill and de Fraine quote the family in support of their correlation of size and structure, while Dr Thomas refers to its members as showing that there is *not* necessarily a close connection between size and structure ((169), p. 731).

Other cases indicating the impossibility of making a comprehensive statement with regard to the correlation of seedling size and structure may be briefly noted.

Amongst the Juglandales and Fagales, in which, as already shown, the arborescent habit cannot be correlated with seedling size, the large seedlings of *Juglans* possess tetrarch roots while those of the somewhat smaller *Carya* seedlings show hexarchy and octarchy; and the much more slender seedlings of *Fagus* have octarch roots. In these cases, therefore, larger size of seedlings is not correlated with the greater number of root poles (Davey(43), pp. 583–595). In the Ranales, Dr Thomas has shown that tetrarchy of the root stele occurs in the small seedling of *Berberis Lycium*, and that a reduction to triarchy takes place in the larger seedling of *B. aristata*; both the tetrarch and diarch conditions are to be found in different individuals of *B. macrophylla* ((169), pp. 701–714). In the Magnolias also, size and structure cannot be correlated.

A considerable range of variation in the number of root poles occurs in different individuals of *Pyrus communis*, a tree, and *Althaea rosea*, a large herb ((169), pp. 723, 724; Bexon(22)); the variations are similar in type in the two species and, in neither case, have they any relation to the size of the seedlings.

Amongst the Sympetalae, Lee has pointed out the impossibility of definitely correlating seedling size and structure in the Compositae ((102), pp. 325–327).

The Monocotyledons have already been referred to, and rejected as a specialised case, in dealing with the correlation between mature habit and size of seedling; but the polyarchy of large seedlings, for example, those of the Palms, may be noted here. There is clearly a necessity for a large initial vascular supply in the generously proportioned seedling, which gives rise, without secondary growth, to

an "arborescent" mature plant; the polyarchy of such Monocotyle-
dons, therefore, cannot be considered as of phylogenetic significance.

While, therefore, in certain restricted circles—for example,
amongst the Leguminosae—there may be correlation between size of
seedling and a particular type of root symmetry, no general rule can
be laid down for the Angiosperms as a whole. As Professor Compton
remarks, characters of seedling structure may be of diagnostic value
to a limited extent, "but it is exceedingly risky to apply them to
solve the broader problems of phylogeny" ((40), p. 118); and though
much work on seedling structure has been done since those words
were written, it is still not possible to use the given data definitely to
decide the primitive habit of Angiosperms; and therefore in this
connection it is needless to speculate on the relative primitiveness of
tetrarchy or diarchy.

It must be noted, however, that the most cogent piece of seedling
evidence concerning the ancestral type of habit for the Angiosperms,
is the general occurrence of a cambium at some stage in the seedlings
of the Ranales, including those of the herbaceous Ranunculaceae.
As already remarked on p. 233, the indications that secondary growth
is inherent throughout this possibly basal group are significant as
suggesting its derivation, as a whole, from arborescent types.

(2) *The comparative anatomy of the stems of trees, shrubs and herbs*

Professor Jeffrey has concluded, from a study of various types
including members of the Ranunculaceae, Nympheaceae and
Saxifragaceae, that the primitive vascular condition for the Angio-
sperms was a solid tubular cylinder, not broken into separate bundles,
the cambium being a uniform and continuous layer (90). This view is
also held by various other American botanists, who criticise the
"Sanio-Sachs-de Bary" description of primary structure and second-
ary thickening in a dicotyledonous stem which appears so generally
in textbooks. This, they contend, implies the development of the
woody type, with a continuous cylinder, from the herbaceous type
with separate bundles; it further implies, therefore, the primitiveness
of the herbaceous habit[1].

[1] See Professor Tansley's criticism of this opinion (163). It is pointed out
that the older botanists did not necessarily intend to suggest the evolution of
woody from herbaceous forms, the phylogenetic standpoint being absent from
their writings. On the other hand, the conception of herbaceous types as the
origin of woody types seems to have existed in the minds of later botanists,
even though it was not definitely expressed; for since the young stages of woody
plants are small and herbaceous in texture, it is only logical to conclude, unless
anatomical investigations are used as a check, that the herbaceous type came first.

These botanists, notably Jeffrey (90, 91, 92, 93, 94), Bailey (10, 11, 12, 13, 15), Eames (46, 47), Sinnott (145, 150, 154) and Torrey (93, 94), have made extensive anatomical studies to demonstrate their contention that the original woody structure of Angiosperms has become modified to produce the structure characteristic of herbs[1].

While the members of the American school are quite in agreement with regard to this point, they differ amongst themselves as to how the modification of the woody cylinder may have been brought about. There are two rival groups, the supporters of the "foliar ray" (or "aggregate ray") hypothesis, and those of the "decrease of cambial activity" hypothesis.

(a) The "foliar ray" hypothesis.

As a result of investigations on the origin of the broad rays in the wood of *Quercus* (46) and on the anatomy of the Rosaceae (47), Eames concluded that the original woody cylinder of the angiospermous stem has become modified by the leaf traces and their influence to produce the separate strands of the herbaceous type. The stages in this process may be summarised as follows:
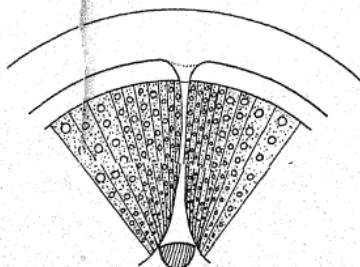
Diagram 2. The aggregation of narrow rays in the neighbourhood of an in-coming leaf trace. (Stippling indicates the presence of fibres.)

(1) The first step in the evolution of the herbaceous type consists in the ordinary narrow rays of the wood of arborescent forms becoming aggregated in the neighbourhood of an in-coming leaf trace (Diagram 2).

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[1] A further list of researches is given in footnotes 4, p. 153, and 1, p. 155. These studies are concerned in general with wood structures. Hemenway's anatomical studies of the phloem of Dicotyledons are also held to support the theory of the derivation of herbs from woody plants (64); the phylogenetic value of Hemenway's work has, however, been questioned by MacDaniels (108), the range of forms studied not having been sufficiently wide.

(2) The vessels in the bands of wood between these aggregating rays disappear (Diagram 3).

(3) The fibres in the tract opposite and flanking the leaf trace become parenchymatised, so that a "broad ray" or "compound ray" is produced[1] (Diagram 4). Such compo··· d rays are at first shallow, not running vertically for any great a ꞵ ⸱ ce.

(4) As the herbaceous condition ƅre mes more established, the foliar rays become more homogeneous ꞓrlyvertically elongated; and the flanking parts become increasingly ɩ ⸲ (ɩinent.

(5) The vertical extension of the foliam ys results in the separation of the original continuous woody cylimheˑ into a series of vascular
                                      ns
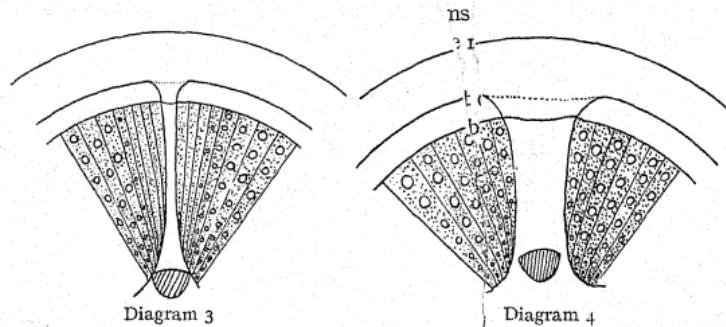
Diagram 3   Diagram 4

Diagram 3. The vessels disappear from the bands of wood between the aggregating rays in the neighbourhood of the leaf trace.

Diagram 4. The fibres subtending and flanking the leaf trace become parenchymatised, so that a broad "foliar ray" is produced.

strands arranged in the ring-like manner characteristic of the stems of herbaceous Dicotyledons (Diagram 5). This stage shows the disappearance of the interfascicular cambium and, in many cases, the loss also of the shallow rays within the remaining wood segments (cf. Diagram 6).

(6) A further modification of the ring of separate strands produces a condition where the cylinder is thinned to such a degree that the *radial* extension of the foliar ray is virtually eliminated.

(7) Finally, by the loss of the fascicular cambium, the "closed

[1] It may be noted that this parenchymatisation of wood segments provided an increased food-storage tissue, rendered necessary, very possibly, under certain conditions of climate, namely the unequal seasonal rainfall and temperature of later geological times. See also the suggestion made by Thompson ((177), p. 1011) that in the Mesozoic period leaves probably persisted for several seasons, so that storage devices would be centred about the leaf traces.

bundle" characteristic, for instance, of *Ranunculus repens* (and of Monocotyledons), may be produced (Diagram 7).

Thus, by the development and ultimate loss of the "foliar ray," the herbaceous type of vascular structure may be derived from the woody type (cf. Diagram 8). The chief botanists supporting this view are Jeffrey, Eames, Torrey (90, 91, 92; 46, 47; 93, 94) and, formerly, Bailey (10, 11, 12, 13); with them are associated various younger workers, communications by Adkinson (1), Flint (50), Gates (54), Holden (84, 85), Thompson (177) and Whitaker (186, 187) being especially noteworthy.
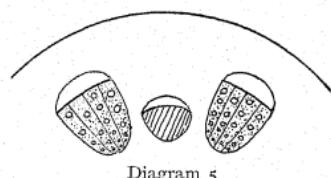
Diagram 5

Diagram 6

Diagram 7

Diagrams 5, 6, 7. Further stages in the evolution of the herbaceous type of vascular structure (for descriptions, see text). It should be noted that while, according to the "foliar ray" hypothesis, the development of the foliar ray initiates the evolution of the herbaceous type, a decrease of cambial activity accompanies the later stages of its development.

Investigations concerning the process of compounding of ray tissues have included a study of:

(1) The comparative anatomy of normal mature plants, many species of different genera and families being considered.

(2) The life history of individual plants.

(3) Those parts of the plant which are generally considered to retain ancestral characters: namely, the seedling, the reproductive axis and the leaf.

(4) Those parts of the plant which may show a reversion to ancestral characters: namely, the first-formed portion of vigorous mature shoots of plants which have undergone vegetative reduction; and traumatic regions of plants.

(5) Fossil material. This, where available, has been used as a check upon phylogenetic conclusions reached by a study of living plants.

One or two interesting points arising from these researches may be mentioned here.

Bailey, working on numerous members of the Betulaceae and Fagaceae (10, 12, 13), confirmed Eames' conclusions that the broad parenchymatous ray is developed by the aggregation and fusion of uniseriate rays and the parenchymatisation of fibres included between them. The genus *Alnus* demonstrates this point. *A. rhombifolia* and *A. maritima* possess the broad parenchymatous ray in the mature wood, although fusion is apparently not complete in *A. maritima*; in the life history of these two species, stages in the aggregation of rays have been disclosed, the seedling having uniseriate rays. This, according to Bailey, indicates that primitive alders possessed only uniseriate rays, such as occur normally in Coniferae and some other Gymnosperms. A consideration of traumatic reactions has led the same author to conclude that the uniseriate ray is the primitive type in oaks also[1].

An interesting set of facts has been contributed by Miss Adkinson with regard to the Vitaceae, a family in which modifications in ray structure may be correlated with habit (1). *Leea* is a tree-like member

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[1] Bailey (11); see also (13). Professor Groom (57, 58) has criticised the view that the broad ray (in *Quercus*, for example) has been built up by the compounding of narrow rays. After a consideration of various data, he suggests the possibility that the small rays of *Quercus* may have originated by the disintegration of primitive wide rays, although he does not believe that it is as yet possible to decide whether the broad or the narrow ray is primitive in this genus ((57), p. 1002). Tabor's investigation of the seedling stem of *Fagus sylvatica* (see reference in (57), p. 1000) shows that disintegration and integration take place side by side in the same annual ring; this indicates that the processes are determined by physiological needs, so that it is unwise to place too much reliance upon them in phylogenetic considerations.

In the light of Professor Groom's criticisms, it is interesting to note that in 1911 Bailey quoted a series of species of *Alnus* to illustrate the compounding of ray tissue; *A. acuminata* is given at the base of the series as possessing uniseriate rays ((12), p. 226). In 1912, however, Bailey mentions the same species as an example in which the uniseriate rays are *not* primitive, but have been produced by the breaking-up and diffusion of compound rays ((13), pp. 655, 657); it is impossible to say, therefore, in what order the series given in the previous paper should be read. (See the notes and diagram on p. 248, concerning the diffusion of ray tissue.)

of the family, while most other types are tendril climbers. If the arborescent habit is primitive for the group, *Leea* may be expected to show the most primitive ray structure; and this, according to Miss Adkinson, is the case, for both uniseriate rays and the production of broad rays are seen in the wood. In all examined species of *Vitis*, except *V. californica*, the uniseriate rays have disappeared from the mature normal wood, though they occur in the seedling and in the leaf segments of the first annual ring; they also reappear after an injury. *Ampelopsis* and *Cissus* have progressed still further, for they have more completely lost the uniseriate ray, while the vascular cylinder is in separate strands. It is, of course, debatable whether much significance can be attached to the behaviour of the wood structures in a family composed so largely of plants having a specialised habit.

As a result of considerable criticism, the foliar ray hypothesis has been restated by Jeffrey and Torrey, who advance in its support further evidence drawn from the nodal anatomy of a wide range of "transitional types," or "woody herbs" (94, 181).

Before consideration is given to the rival hypothesis concerning the method of evolution of herbs, another possibility with regard to the behaviour of the foliar ray should be mentioned.

As stated above, this ray having once evolved, the dissection of the woody cylinder may have continued until the herbaceous type of structure resulted (Diagram 8). In other cases, however, the foliar (= "compound" or "broad") ray may have become modified, and the arborescent, or at least the woody, habit retained. For example, Thompson found that in the Ericaceae the compound rays have become broken up into smaller rays, each consisting of several series of cells—the so-called "multiseriate" type ((177); see also footnote 1, p. 246) (Diagram 8). This multiseriate ray, according to Thompson, was perhaps acquired with the advent of deciduous foliage, when storage centres round the leaves were no longer required; it still, however, provides a good storing capacity, together with a better relation between storing, conducting and mechanical tissues. It was already in existence, as Thompson points out, in the Cretaceous Angiosperms studied by Stopes and Fujii (161)[1].

Miss Holden found that in the Eastern North American members of the Salicales the modification of the ray structures has been carried a step further. While multiseriate rays occur in regions supposedly

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[1] See Sinnott and Bailey's criticism of Thompson's views with regard to the development of the multiseriate ray, noted on pp. 249, 250.

retaining relatively primitive characters, uniseriate rays occur in other parts of the plant (85). Miss Holden also investigated the Sapindales, where multiseriate rays are normal, *Aesculus* alone, of the forms studied, showing reduction to the uniseriate condition in the less conservative regions of the plant (84).

Bailey notes a similar reduction to the uniseriate ray condition in *Castanea, Castanopsis* and *Alnus spp.* amongst the Fagales ((13), pp. 655 *et seq.*).

Structure of
Monocotyledon

Structure of
Herbaceous Dicotyledon

Uniseriate ⟶ Aggregating ⟶ Compound

Multiseriate
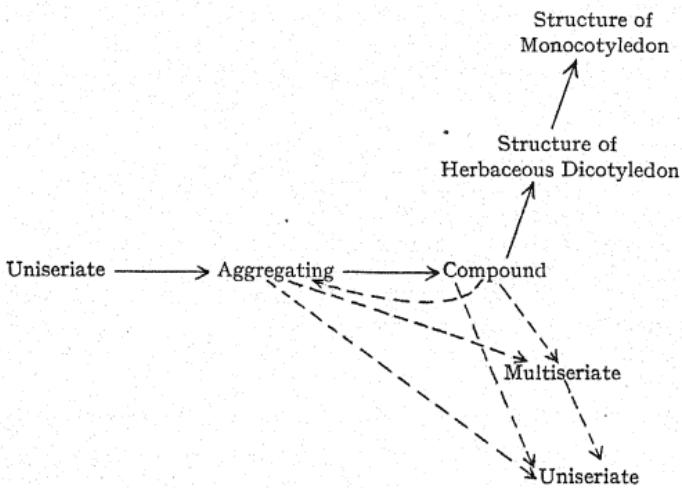
Uniseriate

Diagram 8

Therefore, it is claimed, where the woody habit is retained, the foliar or compound ray, having evolved, may be modified and broken up to produce the multiseriate ray; further diffusion of ray tissue may result in the formation of the uniseriate ray (Diagram 8). It is, moreover, possible that any stage or stages may be omitted in the course of evolution; for example, the multiseriate type of ray may arise directly from the "aggregating" type. Also, both aggregate and compound rays may give rise directly to uniseriate rays; and there is further the possibility that aggregate ray stages may be found in the breaking-up of compound rays (Diagram 8).

(b) *The hypothesis of "decrease of cambial activity."*

Bailey, once so ardent an exponent of the "foliar ray" hypothesis, has in his later work with Sinnott considerably changed his views (150, 151, 152, 15). While still strongly in favour of the derivation

of herbs from woody types, he, with Sinnott, believes that the foliar ray hypothesis is open to objection on various grounds.

In the first place, these authors criticise the great prominence given by Eames to the vascular structure of underground stems in the Rosaceae; they maintain that the use of such stems in determining the factors in the evolution of the herbaceous habit is not legitimate, for in underground organs the absence of mechanical strain and the necessity for storage are liable considerably to modify the structure. Transitions between woody and herbaceous structures should be sought in *aerial* stems, where the actual evolutionary development must have taken place[1].

Secondly, Sinnott and Bailey object to the statement made by Eames, and strongly supported by Jeffrey and Torrey, that the parenchymatised segments of the vascular cylinder have each on their inner border a small primary xylem mass which is a leaf trace, so that the vascular ring consists of alternating large and small bundles. Sinnott and Bailey maintain that in the internode of practically all multifasciculate herbaceous stems, the interfascicular segment of parenchyma has *not* a small leaf trace on its inner margin, and that the stem vascular system is *not* composed of alternating large and small bundles, for the bundles are practically uniform in size[2].

The dissection of the continuous woody cylinder into segments by the development of the foliar ray necessitates the progressive localisation of the primary wood, and such localisation is therefore noted by the advocates of the foliar ray hypothesis as being a distinct feature in the evolution of herbs. Sinnott and Bailey however point out that in certain families composed almost entirely of woody plants, for example, the Araliaceae, Fagaceae, Betulaceae, Proteaceae and others, the ring of primary wood possesses very distinct bundles, while many herbs have a continuous primary ring ((151), p. 555).

In addition to the foregoing general criticisms, Sinnott and Bailey bring forward various other objections to the foliar ray hypothesis, particularly so far as the development of the multiseriate ray is concerned. They point out that multiseriate rays, which are considered by Thompson to be a comparatively recent adaptation to the advent of a severe winter and the consequent acquisition of the

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[1] Cf. the original statement by Eames ((47), pp. 217–220), and criticism by Sinnott and Bailey ((151), p. 555).

[2] See statement by Eames ((47), pp. 219, 224), criticism by Sinnott and Bailey ((151), p. 555), re-statement by Jeffrey and Torrey (94), and support of their criticism by Sinnott and Bailey (154).

deciduous habit, are yet found in Middle and Upper Cretaceous
Dicotyledons. Also, if aggregating and compound rays developed for
the purpose of storing food materials descending from the persistent
leaves of Mesozoic Angiosperms, and were later replaced by multi-
seriate rays as an adaptation to cooler conditions, multiseriate rays
would hardly be well developed in families which have apparently
lived under tropical conditions since ancient times (for example, the
Lauraceae, Anonaceae, Ebenaceae and others)[1].

Sinnott and Bailey maintain that in the cases of tropical woody
Dicotyledons, of Tertiary and Mesozoic woods, and of types adapted
to special habitats (for example, lianes, mangroves, desert plants,
semi-herbaceous shrubs, etc.), there is evidence that multiseriate rays
of considerable width have originated by the gradual widening of
primitive uniseriate rays ((15); (151), p. 558). The widening of narrow
rays may also account for the presence of large rays in roots; these
certainly cannot be explained by the foliar ray hypothesis.

Taking all these facts into consideration, Sinnott and Bailey have
decided that the aggregate or foliar ray hypothesis of the evolution of
herbs is unsatisfactory, perhaps the most cogent objections to it being:

(1) That it is based on a study of nodal anatomy and not on that
of the whole stem.

(2) That it is complicated and indirect, necessitating the develop-
ment and ultimate disappearance of the foliar ray, which is the product
of aggregation of original parenchymatous rays, and "parenchyma-
tised fibres"—that is to say, it is compounded of distinct structures.

(3) That the woody cylinder of trees is frequently unbroken by
foliar rays, while there are a number of herbs which possess a con-
tinuous, though narrow, woody cylinder, foliar rays being absent
((154); (15)).

Sinnott and Bailey therefore propose a more simple and direct
hypothesis to explain the development of the herbaceous type, their
views being supported by the following facts.

In the families Caryophyllaceae, Phytolaccaceae, Hypericaceae,
Lythraceae, Onagraceae, Ericaceae and Polemoniaceae, practically
all the herbaceous forms are characterised by the possession of an
unbroken ring of primary and secondary wood; such a vascular
cylinder occurs also in herbaceous genera of many other families.
The twigs of woody types related to these herbs show a similar con-
tinuous cylinder, wide rays being absent in the secondary wood

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[1] See Thompson's original paper on the multiseriate ray (177), and Bailey
and Sinnott's criticism of his views (15).

(Diagrams 9, 10). Sinnott and Bailey therefore claim that the herbaceous stem "is essentially the first annual ring of the corresponding woody form, with a reduced amount of secondary growth" ((151), p. 558).
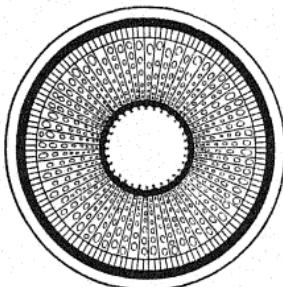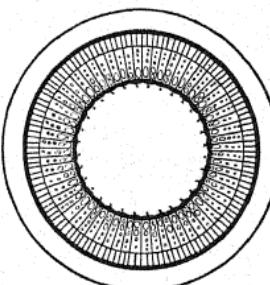
Diagram 9   Diagram 10

Diagrams 9, 10. A woody twig with narrow rays and a continuous protoxylem ring, and a herbaceous stem derived from such a type by simple decrease in cambial activity. (Diagrams from Sinnott and Bailey (151), p. 560.)
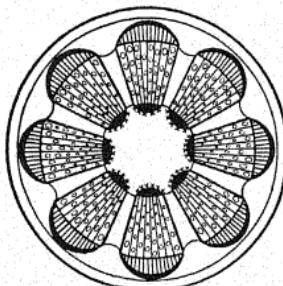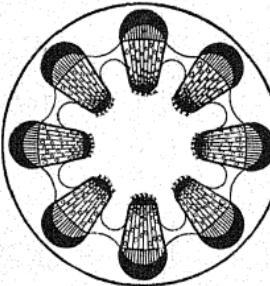
Diagram 11   Diagram 12

Diagrams 11, 12. A woody twig with broad rays breaking the protoxylem ring, and a herbaceous stem derived from such a type by an increase in width of the broad rays, and a decrease in their radial extent. (Diagrams from Sinnott and Bailey (151), p. 557.)

On the other hand, in the case of multifasciculate herbaceous stems of the less reduced type, the interfascicular parenchyma resembles the broad ray of woody plants (Diagrams 11, 12); there is, for example, considerable similarity between the structure of a stout herbaceous stem and that of the first annual ring of *Fagus* ((151), p. 558).

In certain cases, such as *Salvia*, it is recognised that a conversion of segments of the woody ring into fibres or parenchyma has taken place. The process is not, however, comparable with the aggregating and compounding process described by the supporters of the foliar ray hypothesis, for the conversion takes place *between*, and *not opposite*, the protoxylem groups (Diagrams 13, 14) ((151), p. 559).
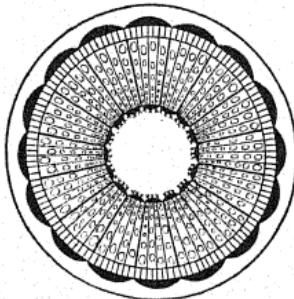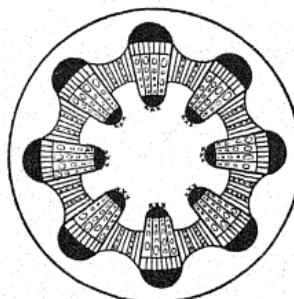
Diagram 13   Diagram 14

Diagrams 13, 14. Woody twig with narrow rays, and a semi-herbaceous stem derived from such a type by partial parenchymatisation of segments *between* the leaf traces; cf. Diagrams 2, 3, 4. (Diagrams from Sinnott and Bailey (151), p. 556. Note that bundles in solid black next the pith represent leaf traces in the stem, and the crosses indicate protoxylem.)

These observations have led Sinnott and Bailey to conclude "that in the development of all herbaceous stems a simple reduction in the amount of secondary wood has been the chief factor"; and this, of course, is due to a decrease of cambial activity. This decrease of cambial activity may be "supplemented by the increase in bulk, to a greater or less degree, of the ordinary parenchymatous tissue"; and this increase of parenchyma, in its turn, may be the result of simple widening of primitive uniseriate rays. Further decrease of cambial activity would, of course, ultimately lead to the monocotyledonous type of vascular structure.

The main point to be emphasised in the anatomical study of the evolution of herbs is that an herbaceous stem in all its essentials is like the first annual ring of its woody relatives. If this has a continuous ring of primary and secondary wood, as do the twigs of woody species of *Nicotiana*, *Hypericum*, and *Hibiscus*..., the corresponding herbaceous stem will show the same features.... If the woody form possesses wider rays and an interrupted primary cylinder, as does *Xanthorrhiza* and the arborescent species of *Acanthopanax* and *Senecio*...its herbaceous representative will show but a slight

exaggeration of the same thing.... The whole process of reduction from a woody to an herbaceous condition is therefore a very simple and natural one ((151), pp. 559, 560).

Diagrams 9, 10, and 11, 12, illustrate this hypothesis of the development of the herbaceous type.

It will thus be seen that a study of the comparative anatomy of Angiosperms as outlined above favours the derivation of herbs from woody plants, whether the matter is regarded from the point of view of Jeffrey and his collaborators, or from that of Sinnott and Bailey.

The significance of the inferences from the two hypotheses should be noted. Jeffrey and Torrey point out that if herbaceous Angiosperms have resulted from a decrease of cambial activity, they are *degenerate* ((94), p. 246); and the large development of herbs within the group would therefore indicate that it has passed its zenith and is slowly declining in a manner comparable to that suggested in the case of the Equisetales and Lycopodiales. If, on the other hand, herbaceous Dicotyledons are the result of active advance and differentiation, as Jeffrey and Torrey maintain, they are not degenerate, but *dynamic*, possessing the capacity for further adjustment, modification and evolution.

Mrs Arber's recent work(6) considers the feature—*woodiness*—which, apart from size, especially distinguishes trees from herbs, in a light very different from that of the American botanists, particularly the exponents of decrease of cambial activity.

Mrs Arber asks: "What is the significance of woodiness?" and finds her answer in Church's view that "the transference of plant life from the sea to a subaerial environment, with its intensive insolation, and its relatively inadequate supply of salts, leads to an accumulation of photosynthetic products; the plant under these changed conditions stores sugars, starches and celluloses, because it manufactures them in undue quantities and does not know how to dispose of them" ((6), p. 81). One result of all this accumulation of non-living material is the timber tree (cf. Church(38), pp. 78, 79).

Attention is drawn to the fact that palaeontologists regard the accumulation of non-living-material in the animal body as an indication of racial old age; and Mrs Arber suggests that the same may hold good for plants also; so that trees, with their masses of non-living substance, namely woody tissue, are expressive of racial senile degeneration, and must, according to this view, be regarded as a later development within any plant group than the herbs with their much smaller bulk of non-living substance.

Mrs Arber further holds that the frequency of the tree habit in the Angiosperms points

> to the extreme antiquity of the flowering plant stock, which has allowed time for many lineages to reach a phase of senility;.... The tree habit is probably the outcome of a certain fundamental tendency, which is the compensatory drawback to the capacity for photosynthesis—the liability to the accumulation of waste products. It may be hazarded that the earliest symptom of this tendency, historically, was the deposition of a wall round the plant cell;.... The same tendency may be held to have reached an ultimate expression in the massive framework of the forest tree ((6), p. 83).

According to Mrs Arber's view, therefore, it is the *trees*, with their accumulations of non-living, waste material, which are the "degenerate" types amongst the Angiosperms—not the *herbs*, as the hypothesis of decrease of cambial activity would indicate. The herbs represent the earlier habit-form for the group; and it is the frequency of trees, rather than of herbs, which, for Mrs Arber, would indicate that amongst Angiosperms there are at least many forms which have passed their zenith.

Mrs Arber assumes, for the sake of simplicity, that the Angiosperms are monophyletic in origin, so that the primaeval Angiospermstock must have been *either* herbaceous *or* arborescent; for her, it is most logical to believe that it was herbaceous. But the group was not necessarily derived from a pro-Angiosperm stock of homogeneous habit; it may have developed along various lines from a stock which *already* contained both herbs and woody forms. So that, while the logic of the claim for *ultimate* primitiveness of herbaceous types is indisputable, neither herbaceousness nor woodiness is necessarily *immediately* and exclusively primitive for the modern Angiosperm group as a whole.

While, *within the group*, herbs may have given rise to woody plants by the accumulation of "waste material," woody plants, on the other hand, may have given rise to herbs, or at any rate herb-like plants, by some process such as that suggested by Sinnott and Bailey in their hypothesis of decrease of cambial activity. As Dr Willis points out, with reference to such genera as *Hypericum, Senecio,* and others containing both herbs and woody forms, "It is evident that for nature to form a tree from a herb or shrub, or *vice versa,* is not a specially difficult or unusual feat" ((195), p. 47).

An important point, however, arises out of this statement by Dr Willis.

Mrs Arber asks ((6), p. 74) whether there are "any herbs which in themselves give evidence of a tree ancestry," and in answer to the question draws attention to an investigation made by Dr Burtt Davy (44). This author describes certain sub-shrubs and "herbs" from the High-veld of the Transvaal; and since these plants belong to genera which are represented elsewhere exclusively by woody plants, he regards them as transition types in the evolution of herbs from trees under special environmental conditions. After an examination of evidence concerning three of these plants—*Eugenia pusilla, Erythrina Zeyheri* and *Menodora heterophylla*—Mrs Arber finds that they are essentially woody, though greatly reduced, so much so that their woody development may be almost entirely underground; they are not strictly herbaceous, and cannot, therefore, be accepted as evidence in support of the derivation of herbs from woody plants. On the other hand, Mrs Arber claims that they form an illustration of Dollo's "Law of Irreversibility" (4, 5), according to which "no species in the course of its evolutionary development ever really retraces its steps; it may return to something superficially resembling a stage which it has passed through, but the later is never an exact reincarnation of the earlier stage. On this law we should suppose that if the primaeval Angiospermic stock was herbaceous, a tree lineage arising from this stock might eventually be reduced again to something resembling a herb, but it would not achieve the herbaceous habit with any exactitude; and this seems to be what has happened in the case of these shrublets of the High-veld" ((6), pp. 75, 76).

In view of Mrs Arber's criticism, an anatomical re-examination of stages in the life history, conservative regions, traumatic reactions, etc., would be interesting in the case of those types quoted by Sinnott and Bailey in support of their hypothesis of decrease of cambial activity. It may be that the various series, or at any rate some of them, would reveal increasing, instead of decreasing, woodiness; while other series might show that the "herbs" included in them are really reduced arborescent forms.

(3) Leaf form, and the vascular supply to the leaf

Sinnott and Bailey claim that the palmate leaf, probably of lobed outline, represents the primitive type for Angiosperms, and that the pinnate varieties, dominant in recent floras, are derived types (152). Data in support of this view are drawn from conservative regions of the plant, from palaeobotanical evidence, and from phylogenetic considerations, and may be summarised as follows.

(1) Floral leaves (sepals, petals and bracts) are often palmately veined, even in plants where the foliage leaves are pinnately veined, while cotyledons are palmately veined in the majority of Dicotyledons ((152), pp. 8, 9; figs. 25–69). These facts point to palmation as an ancient character persisting in organs generally recognised as conservative.

(2) In present-day floras, varieties of the pinnate type of leaf (particularly simple pinnate) are undoubtedly dominant ((152), p. 3, Table 1), while Sinnott and Bailey claim that from available palaeobotanical evidence, palmate leaves, particularly of lobed outline, appear to have been represented in greater proportion in Cretaceous and Tertiary floras than at the present time ((152), p. 5, Table 2)[1]; this would, of course, indicate that they are the older type.

(3) An examination of the distribution of leaf type amongst the recent members of Angiosperm families shows that the simple pinnate leaf is overwhelmingly predominant in the Metachlamydeae, with their advanced floral morphology; while amongst the Ranales, Rosales and Malvales, considered by some phylogenists to possess the primitive type of floral morphology for the group, palmate leaves, particularly of lobed outline, occur with great frequency ((152), pp. 10–13). In the absence, however, of conclusive evidence as to which group of the Archichlamydeae really presents the most ancient reproductive morphology, this last point must be accepted with caution; for amongst the "Amentiferae," the rival claimants to floral primitiveness, pinnate leaves of various types occur in large proportion[2].

In a separate communication, Sinnott gives an account of the nodal anatomy of a large number of Dicotyledons (145). A foliar supply of three strands, each causing a gap in the stem vascular cylinder, and consequently producing a "trilacunar node," appears to be characteristic of most Dicotyledons, particularly those of the Archichlamydeae((145), pp. 319, 320) (Diagram 15). Sinnott therefore regards the trilacunar node as being of at least ancient origin in the group, and as constituting a basal type[3]. It is shown that this basal

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[1] Note that even in these ancient floras, pinnate leaves are the predominant type; cf. the examples figured by Berry (17).

[2] Note that Sinnott and Bailey do not accept the idea of primitiveness of the "Amentiferae" in discussing the primitive type of foliage leaf ((152), p. 11). In connection, however, with their claim for the primitiveness of the "trilacunar node," they mention the group as being amongst the "relatively ancient" Dicotyledons, associating them with the Ranales, Rosales and Malvales ((152), p. 6).

[3] It should be noted that in the Cycadophyta, a unilacunar node appears to represent the primitive state, the dilacunar condition of recent Cycads being a later development (Wieland (189), vol. 1, pp. 66, 67).

type may have been modified both by reduction and by amplification. Reduction by fusion of the three original traces seems to have occurred in the Centrospermae and Tubiflorae; while reduction in the Ebenales, Ericales, Contortae and others has probably taken place by suppression of the two lateral traces. In these cases, a single gap is left in the stem vascular cylinder, and a "unilacunar node" is produced (Diagram 16). Such a node occurs in large proportion amongst the Metachlamydeae ((145), p. 320). A multilacunar node is the result of amplification, that is, of a division of the three original traces; this is found in the Polygonales and Umbelliflorae. Uni-, tri- and multilacunar nodes occur in the Ranales and Rosales, particularly

Diagram 15   Diagram 16

Diagram 15. A typical modern palmate lobed leaf with cross section of the node (from Sinnott and Bailey (152); see Fig. 84). "The node is trilacunar but the traces are pulled closely together in a narrow petiole before separating again in the lamina."

Diagram 16. A pinnate simple leaf arising from a unilacunar node (from Sinnott and Bailey (152); see Fig. 85); "the single trace continues as a strong midrib."

in the families Trochodendraceae, Magnoliaceae and Rosaceae; these are evidently plastic groups so far as nodal anatomy is concerned.

Sinnott and Bailey find a considerable degree of correspondence between leaf venation and nodal anatomy ((152), p. 7, Table 4)[1]; and they make a reasonable claim for a broad correlation, on the one hand, between the palmate leaf type and the trilacunar node—two characters which they believe to be relatively primitive (Diagram 15); and, on the other hand, between the pinnate leaf type and the uni-lacunar node—derived characters, the evolution of which may have been determined by the origin of the petiole (Diagram 16) ((152),

[1] See also Sinnott and Bailey's work on the correlation of stipules with the trilacunar node (150).

pp. 13, 14). This "may well owe its development to the fact that the early Angiosperm leaf, ever increasing in breadth of lamina, was in need of a greater flexibility than was afforded by a broad sessile base...." "The primitive leaf with its three traces widely separated in origin passing directly from node to lamina was thus constricted at its base and its three bundles forced close together in the petiole" (cf. Diagrams 15, 17). The petiolar system "seems to have shown an increasing tendency to persist as a single strand," this forming the single midrib of the lamina, and giving off lateral branches in a pinnate manner (Diagram 16).

Diagram 17. Reconstruction of the leaf and node claimed by Sinnott and Bailey ((152) to be primitive for the Angiosperms. "The node is trilacunar and the veins depart directly into the lamina without approximation in a petiole."

If the suggestions made by Sinnott and Bailey with regard to leaf type and nodal anatomy be admitted, an attempt at further correlation of these characters with habit of growth may yield useful evidence concerning the habit of primitive Angiosperms.

It has already been noted that varieties of the pinnate leaf are strikingly predominant amongst the Angiosperm floras of the present day. They occur, for example, in the arborescent types of the Salicales, Juglandales and Fagales; in shrubby types, such as *Rosa* and *Philadelphus*; and in herbaceous types amongst the Caryophyllaceae, Scrophulariaceae, Campanulatae and Compositae; while they are the general rule amongst the herbs, shrubs and trees of the Leguminosae. The predominance of pinnate leaves thus makes it impossible to correlate them exclusively with any particular habit of growth. It is equally impossible to refer palmate leaves, as a whole, to either woody or herbaceous plants; for they are to be found in *Cercis* and the Maples (trees), in *Ribes* and *Lavatera* (shrubs), and in *Caltha, Delphinium, Saxifraga, Geranium, Malva* and other herbs.

A consistent correspondence between nodal anatomy and habit is also difficult to discover, as will be seen from the following evidence drawn from Sinnott's tabulated summary of nodal type ((145), pp. 319, 320).

While such woody forms as those of the Salicales and Fagales are trilacunar, and such herbaceous forms as those of the Centrospermae and Tubiflorae are unilacunar, numerous discrepancies occur in other groups. For example:

(1) Both herbs and shrubby climbers of the Piperales are tri- and multilacunar.

(2) Herbs, shrubs and trees of the Urticales are as a whole trilacunar.

(3) Amongst the Ranales, the woody Trochodendraceae and Magnoliaceae are uni-, tri- and multilacunar; the herbaceous Ranunculaceae are tri- and multilacunar; while the Anonaceae, Lauraceae and other woody families are unilacunar.

(4) Amongst the Rosales, the herbs, shrubs and trees of both the Rosaceae and Leguminosae are mainly trilacunar; the woody Hamamelidaceae are trilacunar, while the tree forms of the Eucommiaceae are unilacunar.

(5) The woody members of the Sapindales show slightly more unilacunar than trilacunar types.

(6) The Primulales, herbaceous and woody, are all unilacunar; while

(7) The herbs and shrubs of the allied order, Plumbaginales, are trilacunar.

(8) The arborescent Ebenales are unilacunar; and

(9) The typically herbaceous Plantaginales are trilacunar.

(10) The herbs and climbers of the Cucurbitales are trilacunar.

(11) Amongst the Campanulatae, the herbs and woody forms of the Campanulaceae are unilacunar; while the Compositae, a mainly herbaceous family, are mostly trilacunar.

At first sight, therefore, it does not seem possible to establish—between the separate characters of leaf type and nodal anatomy on the one hand, and habit on the other—correlations throwing any light on the primitive growth form of the Angiosperms. The detailed investigations of Sinnott and Bailey, however, reveal the following points:

(1) There is a general association between palmate *simple* leaves and a tri- (or multi-) lacunar node amongst woody plants, though such an association is not so frequent amongst herbs ((152), p. 7).

(2) Practically all the palmate *lobed* and palmate *compound* leaves (as well as a large number of pinnate compound leaves) belong to tri- (or multi-) lacunar species in both woody and herbaceous plants ((152), p. 7).

(3) Amongst woody plants, the trilacunar node predominates only in temperate regions (for example, in the Salicales); in tropical woody plants, the unilacunar node is the more frequent (for example, in the Ebenales) ((152), pp. 15–17).

(4) Amongst woody plants, the palmate lobed leaf is almost entirely confined to temperate regions ((152), pp. 15–17).

The trilacunar node and the palmate lobed leaf appear, therefore, to be linked with the arborescent habit in temperate regions, at least; and this may perhaps be considered as a point in favour of the primitiveness of tree forms in such regions.

The apparent inconsistencies in the correlations of leaf form, nodal anatomy and habit, may be explained by the fact that while various characters may evolve side by side in large groups as a whole, not all the characters evolve together, or at the same rate in different individuals of the group; one character may lag, another proceed rapidly, in different cases, and under different climatic conditions. For example, Sinnott and Bailey suggest that the many species (such as those of the woody Fagales), in which a trilacunar node is associated with the pinnate form of leaf, illustrate "the persistence of an ancient character at the node, which has been lost elsewhere in the leaf" ((152), p. 8). With regard to the effect of climatic conditions, an example may be provided by the development of the unilacunar node in tropical woody plants. This has perhaps been accelerated by the evolution of the large and heavy leaf with its stout, rounded petiole, suited to tropical rain-forest conditions. The point of attachment of such a petiole is circular, instead of elongated as in most woody plants of temperate regions; and this rounded leaf insertion has very probably brought about the concentration of the leaf supply and the development of the unilacunar node ((152), p. 14).

The results of their regional or climatic survey of venation, leaf type and habit, combined with those of their anatomical and other researches on the primitive habit of the Angiosperms, have therefore led Sinnott and Bailey to the conclusion that early Angiosperms were woody plants with trilacunar nodes and palmate leaves, probably of lobed outline (Diagram 17); and that they evolved under temperate upland conditions in early Mesozoic times. Further suggestions made by these writers with regard to the development of the group, are

that the main stages of foliar evolution took place while the Dicotyledons were still predominantly woody; that Angiosperms sprang from a palmate coniferous stock, with sessile leaves of the *Araucaria* type, rather than from a pinnate cycadean stock; and, finally, that Monocotyledons, with their parallel venation, were derived from a palmate group of Dicotyledons, very likely at an early stage of Angiosperm evolution, when the palmate leaf was predominant.

(4) *Flower type and habit*

The Ranales, with perfect flowers, and the comprehensive group "Amentiferae," with typically more simply constructed flowers, are rival candidates for the distinction of being considered the most primitive of existing Angiosperms. In either case, the evidence seems to support the hypothesis of the arborescent, or at least woody, nature of primitive Angiosperms[1].

Further, in many instances of orders, families, and even genera containing both woody and herbaceous species, it is possible to distinguish the more primitive—from the floral point of view—from the more highly developed members, and to correlate these floral types with habit. For example, in the Umbelliflorae, the fixed floral plan of the Umbelliferae is correlated with the herbaceous habit, while the more varied, and therefore presumably more primitive, floral structure of the Araliaceae accompanies the woody habit (Sinnott and Bailey (151), p. 563).

In the Leguminosae, 113 of the genera of the two sub-families Cesalpinioideae and Mimosoideae are entirely woody, while the remaining eight genera contain both woody and herbaceous forms. The floral structure of these two groups is generally admitted to be more primitive than that of the Papilionatae which contains a much larger proportion of herbaceous forms ((151), pp. 562, 563). The Compositae, again, with their very advanced floral organisation, consist largely of herbs, there being only 1·5 per cent. of shrubby or arborescent types[2].

The Violaceae provide another example of the broad correspondence between floral structure and habit, for those members of the family which have simple, regular flowers are woody in structure;

[1] See references given in footnotes 2 and 3, p. 154; and note especially the seedling evidence suggesting the primitiveness of woodiness for the Ranales as a whole.

[2] Small(155); note that Worsdell(196) interprets the structure of the Compositae as indicating that the herbaceous habit is primitive for the family, a few members of which have become woody; cf. this view with the inferences drawn by Sinnott and Bailey.

the Violeae, with their markedly zygomorphic, and therefore presumably more advanced, flowers, are herbaceous ((151), p. 563).

In the genus *Potentilla*, also, those forms in which the floral structure is considered to be the least advanced are shrubs or undershrubs, while the higher members, from a floral point of view, are all herbaceous ((151), p. 563). Other instances of the same kind occur, amongst individual families or genera, pointing, according to Sinnott and Bailey, to the greater antiquity of the woody type amongst Angiosperms. Mrs Arber ((6), p. 79) adds a further example from the Gramineae, noting that while grasses have usually very reduced flowers, the dendroid Bamboos have flowers which approximate more nearly to the typical monocotyledonous plan; but, as will be shown later, Mrs Arber interprets the correlation of flower type and habit in a different way from Sinnott and Bailey.

Further, if the Dicotyledons are viewed as a whole, 68 per cent. of the genera of the Archichlamydeae are found to be woody, while amongst the Metachlamydeae or Sympetalae, with the more advanced type of floral organisation, more than half the genera are herbaceous. Also, it is an interesting and suggestive fact, according to Sinnott and Bailey, that of the 35 entirely herbaceous families of Dicotyledons, the great majority can have no possible claim to primitiveness, for they are either parasites (Rafflesiaceae), water plants (Callitrichaceae), insectivorous plants (Droseraceae), or they are monotypic (Adoxaceae) ((151), pp. 564, 565).

Sinnott and Bailey therefore conclude that a study of the distribution of herbaceous and woody types in the general system of classification is distinctly in favour of the primitiveness of the arborescent habit amongst Angiosperms.

As already noted, however, Mrs Arber has suggested another interpretation of the correlation of flower type and habit ((6), pp. 77–80). Drawing attention to the shortness of generations in herbs as compared with those in trees, this author notes that "the herb will, in theory, have more numerous chances of exhibiting mutations than the tree. And that this is what has actually taken place, in practice, is shown by statistics of the relative number of species in genera and families of trees and herbs; for it is clear that the existence of a relatively high number of species in a genus or family means that it has been the scene of correspondingly active evolutionary development. Sinnott shows that in the Dicotyledons the average number of species in the woody genera is 12·5, while in the herbaceous genera it is 15. When we reckon by families the difference is more striking, for

the woody families average 310, and the herbaceous 510 species to a family. The existence of this *evolutionary lag*—if we may so name it—among trees as compared with herbs is clearly expounded by Sinnott, and yet he hardly seems to appreciate its full significance." According to Mrs Arber, the facts quoted by Sinnott and Bailey in favour of the primitiveness of arborescence, may be explained as due to evolutionary lag, the "necessary outcome of the tree habit." In the case of the Leguminosae for example, especially referred to by Sinnott and Bailey as illustrative of their view, Mrs Arber believes it "more logical to suppose that (they) were originally herbaceous, and that those lineages which adopted the tree habit, put a break, as it were, upon their own evolution, and thus dropped behind the lineages which, by remaining herbaceous, retained the power of mounting the ladder of floral specialisation at a relatively rapid rate."

In connection with a consideration of flower type as correlated with habit, Mrs Arber also draws attention to the work of Ischikawa (89), who, from a general correlation of aberrant embryo sacs with plants of herbaceous habit, argues in favour of the derived nature of such plants. Mrs Arber believes that Ischikawa's evidence is insufficient to allow of its use in this connection; but if it is true that aberrant embryo sacs do occur almost exclusively in plants of herbaceous habit, then her explanation of the more advanced floral structure of herbs may be applied also to cytological details.

(5) *Fruit type and habit*

According to Sinnott and Bailey, Angiosperms with fleshy fruits are very generally of arborescent, shrubby or climbing habit; the dispersal of seed in such cases is usually by the agency of birds, as, for example, in the Rosaceae. Terrestrial herbs, on the other hand, are largely characterised by the possession of dry fruits and seeds, dispersal being effected by explosive and censer mechanisms, or by the agency of the wind, as in *Geranium, Papaver, Taraxacum,* and many other types (153). Sinnott and Bailey suggest that since frugivorous birds are generally reluctant to feed on the ground[1], the dry fruits of low-growing plants have been developed to meet the needs of seed dispersal. They assume, therefore, a change in fruit type correlated with the change in plant habit from woody to herbaceous. Sinnott further correlates these changes with the

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[1] Note, however, the damage done to strawberry crops by thrushes and blackbirds.

increase, perhaps even the origin, of ground-feeding birds, such as finches[1].

Fleshy fruits, or rather seeds, seem to have characterised the extinct Gymnosperms, as well as the more primitive living members of the group. They are, therefore, at least of ancient origin; and if their association with primitive Gymnosperms is an index of their own primitiveness, then their occurrence in woody Dicotyledons, such as the Rosaceae, may perhaps signify the primitiveness of the woody habit in Angiosperms. The correlation of fruit type and habit must, however, be made with caution, for dry, wind-dispersed fruits and seeds occur, for example, in *Salix, Populus, Alnus, Betula, Carpinus* and *Ulmus* of the "Amentiferae"; in *Liriodendron* of the Magnoliaceae, and in *Platanus*; also in *Acer, Fraxinus* and the majority of the members of the woody family Bignoniaceae, such as *Catalpa*. Thus dry fruits occur amongst woody Angiosperms which are variously regarded by different writers as primitive, as well as amongst types generally considered to be more advanced. Moreover, many of these genera are of relative antiquity, and their characteristic fruits are known in fossil form, as in the case of *Populus, Betula* and *Acer*; while wind-dispersed winged seeds are associated with the arborescent habit in the Pinaceae amongst Gymnosperms. This frequent occurrence of dry fruits and seeds amongst woody plants indicates that if there has been a change in fruit type, as Sinnott and Bailey suggest, it is a change which has taken place irrespective of habit, and therefore it cannot be said to mark, or to coincide with, the development of herbaceous forms amongst Angiosperms.

Further, it may be pointed out that though fleshy fruits are not very commonly found amongst low-growing plants, they occur, for example, in *Actaea* (Ranunculaceae), in *Fragaria* (Rosaceae) and in *Solanum*; also amongst Monocotyledons, in the Asparagoideae, in *Haemanthus* and certain other Amaryllidaceae, while in *Iris foetidis-*

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[1] Sinnott (146), p. 297. In this paper, interesting suggestions are made concerning the result of the evolution of herbs. The author is of the opinion that the large development of herbaceous Angiosperms "which has taken place for the most part since the beginning of Tertiary time," has not only had a far-reaching effect upon the aspect of vegetation, but that it has been a determining factor in various lines of development within the animal kingdom, having had, for example, an important relation to the evolution of herbivorous mammals and of ground-feeding birds. Moreover, he suggests that "human society is essentially an herbaceous product," for one of the first steps of primitive man towards civilisation was "to enter the open" and take up agricultural pursuits. The quickly-growing herbs would be the most likely plants to be selected for cultivation; while the practice of animal husbandry is dependent upon herbaceous vegetation ((146), pp. 297, 298).

sima, the seeds possess a fleshy bright-coloured testa. Fleshy fruits and seeds are represented, therefore, in groups considered to be relatively primitive, and also in more advanced types; and it is impossible to say whether or not these latter cases are examples of the retention of a primitive fruit type.

It appears, therefore, that, in the present state of knowledge, a consideration of fruit type contributes little or no evidence of value concerning the primitive habit of Angiosperms.

VI. Suggestions concerning future investigations on the primitive habit form of Angiosperms

It may be well to conclude this examination of evidence concerning the primitive habit form of Angiosperms by indicating some of the lines along which future investigations on the comparative development of herbs and woody plants may be carried out.

It is only too easy to speak glibly of the effect of changed ecological conditions on the physiological needs of the plant, and to conclude, for example, that the compound ray is a result of the need for increased storage tissue to tide the plant over periods unfavourable to the actual manufacture of food materials; and that the ultimate evolution of the herbaceous habit enables the plant to perennate underground, or in the form of seeds, between growing seasons. It is not intended to imply that these are not legitimate conclusions; but they are apt to be applied to the Angiosperms as a whole, without a real understanding of the structure of the individual plant as determined by its own physiological needs; or without comprehension of the sequence of events which led to the differentiation of its various tissues.

It is necessary, as Professor Tansley has pointed out, to "approach structure through development, the mechanics, physics and chemistry of growth and differentiation"; and to realise that process or function "creates and modifies structure," and is also "in its turn determined by structure." A study of pure morphology alone can never explain structure; a study of process also is necessary[1].

The methods available in a study of "causal morphology" were outlined by Professor Lang in 1915 in his Presidential Address to Section K of the British Association, as follows:

(1) The detailed study in selected plants of the normal development and its results.

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[1] Tansley (164), pp. 257–259; cf. Bower ((26), p. 169), "the problem of evolution is in its essence physiological." See also Bews (19, 20).

(2) Comparison over as wide an area as possible, with special attention to the essential correspondences arrived at independently.

(3) The study of variation, mutations and abnormalities in the light of their development.

(4) Critical experimental work ((98), p. 704; see also (99)).

A very considerable amount of work has already been done along these lines by Professor Priestley and his collaborators, on the differentiation of endodermis, cork, cuticle and conducting-tissues ((120, 121, 122, 123); see also (124, 125, 126, 127, 128, 157)); by Petersen (115) and by Kostytschew (97) on the differentiation of vascular bundles in the individual; by Professor Thoday on the comparative structure of sunflower stems of different ages and sizes (167); by Professor Holden and his assistants on abnormal seedlings ((78); see also (79, 83, 21)); by Professor McLean Thompson on the developmental morphology of floral structures (109, 110, 111); and by various members of the American school, on physiological and morphological correlations (14, 54, 100, 187, 188, 93).

Work along these lines—and there is still much waiting to be done—will lead to a better understanding of the real causes and determining factors in the development of forms and structures, which, from the purely morphological standpoint, are already familiar.

VII. Summary

The foregoing examination of evidence concerning the primitive habit form for the Angiosperms shows that along certain lines of enquiry the present state of knowledge is so inadequate and inconclusive that no conjecture can reasonably be made from it. This is the case with regard to evidence from the fossil record of the group, and from a consideration of its various fruit types.

Along other lines, the evidence may be suggestive of the primitiveness of either one or the other habit form, though in these cases it is difficult to avoid assumptions and pre-conceived ideas in interpreting the evidence. For example, in a consideration of climatic and geographical distribution of the habit forms amongst the Angiosperms—the results of which are interpreted differently by different writers—there is a tendency, in some cases at least, to assume that plant type and climate were correlated in past ages in the same way in which they are correlated to-day; and this is not necessarily the case.

Taken simply on its own merits, an examination of seedling anatomy is entirely unproductive of decisive evidence concerning the primitive habit of Angiosperms. If, however, the primitiveness of the

Ranalean floral plan is accepted and taken as indicative of the basal position of the order amongst Angiosperms; and if Angiosperms are further assumed to be monophyletic, then the idea of primitiveness of arborescence for the whole group is suggested by the invariable presence of a cambium in the seedlings of the Ranales. Moreover, the same idea having been developed (whether legitimately or not) from such considerations as a comparison of Angiosperms with other plant-phyla, and surveys of their fossil record and of their geographical distribution, it may be held that herbs have developed from trees by, for example, a decrease of cambial activity.

On the other hand, on the single assumption that the Angiosperms are monophyletic, so that the ancestral form must have been *either* herbaceous *or* arborescent, it may very cogently be argued, from various other standpoints, that herbs are primitive and trees derived within the group, the development of tree forms having taken place by the accumulation of non-living woody material. The arguments upon which this view is based are drawn, notably, from enquiries into the significance and cause of the accumulation of woody material, and into the frequent correlation of simple flower type with the tree habit, this latter being explained by the slower maturation of trees, with their consequent longer generations and curtailed opportunities for floral evolution.

It will be realised that the arguments used to determine the primitive habit form of the Angiosperms are, for the most part, highly conjectural; and the fact remains that it cannot as yet be decided, either from direct evidence or from the vast amount of speculative evidence which has been advanced by different writers, what the habit form of the first true Angiosperms really was. Under the circumstances, it is only very tentatively that another suggestion is added to the list: namely, that at some early period, when the predecessors of modern Angiosperms were being differentiated, *both* trees and herbs were represented in the Pro-Angiosperm stock, so that neither type can be considered as *immediately* primitive for the group as a whole. Within the modern group, originally herbaceous stocks may have produced trees, and members of arborescent stocks may have been reduced to herb-like forms. A knowledge of the original habit for circles of relationship can only be further advanced by comprehensive physiological and anatomical studies of the developmental history of individual types; and ultimately, perhaps, such knowledge may indicate what was the composition, with regard to habit, of the ancestral Angiosperm stock.

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NOTE

Reference should be made to a discussion on "The Antiquity and Early Evolution of the Angiosperms" at the recent International Botanical Congress held at Cambridge, August 16–23, 1930. Dr Hamshaw Thomas re-stated his view that the evolutionary tendencies already detected in the Pteridosperms, Caytoniales and Bennettitales "furnish reasonable grounds for the idea that the Angiosperms were derived from various Pteridosperms early in the Mesozoic period." In reviewing the earlier Mesozoic floras for indications of Angiosperm-like structures, Dr Thomas commented upon the paucity of evidence with regard to stem structure, and referred to Professor R. Kräusel's recent description of *Suevioxylon zonatum,* a wood of Jurassic age from Württemberg, showing dicotyledonous characters (Paläobotanische Notizen, XI. Über ein Jura-Holz vom Angiospermentypus. *Senkenbergiana,* **10**, 250, 1928). During the discussion Professor Sahni exhibited a specimen of a fossil wood from the Rajmahal Hills (India); this wood is of great interest, as it is probably of Lower Jurassic age, and is, moreover, similar in structure to that of the Magnoliaceae. It therefore points not only, as does *Suevioxylon,* to the antiquity of the woody habit amongst plants of Angiosperm type but also to the antiquity of the Magnoliaceous type.

It may be noted here that a valuable summary of Dr G. R. Wieland's views regarding the origin of the Angiosperms will be found in the *Proceedings of the International Congress of Plant Sciences (Ithaca),* **1**, 429, 1929.

NOTE ON THE EFFECT OF GROWING MOSSES IN A MOISTURE-SATURATED ATMOSPHERE, AND UNDER CONDITIONS OF DARKNESS

By W. LEACH

(With 3 figures in the text)

THE marked structural modifications such as reduction in leaf size, and increased elongation of the axis, exhibited by mosses and liverworts when brought into the laboratory and grown in closed glass vessels under conditions of reduced illumination are well known. The often striking nature of these modifications led me to grow a number of mosses in complete darkness, with a view to determining to what degree the changes in form and structure could ultimately be carried.

It was originally intended to attempt to investigate the effect of darkness alone, but the difficulty of controlling atmospheric humidity in any way other than by maintaining it at a maximum value, and at the same time keeping the plants in a healthy condition, led to the abandoning of this idea. The plants were therefore grown at ordinary laboratory temperature in a moisture-saturated atmosphere and in darkness and, although it was not found possible to determine with any certainty the effects of each individual operating factor, the results yielded were interesting in a number of ways.

Very little work appears to have been published regarding etiolation phenomena in mosses. Since this work was begun, however, a note by de Virville[1] upon the subject has appeared. De Virville claims to have controlled light, temperature, and humidity, and he describes a number of effects produced by his experiments which he puts forward as being due to darkness or diminished light intensity. Some of these effects are precisely similar to those arising in my experiments, where plants were kept in the laboratory in closed vessels and exposed to full daylight. It seems therefore likely that many of de Virville's results are humidity effects. That is, they are due to the fact that his plants were kept under conditions of uniform humidity instead of undergoing the alternate desiccation and soaking that they always experience under natural conditions.

[1] de Virville, Ad. Davy. Action de la lumière sur les Mousses. *Comptes Rendus de l'Acad. des Sc.* 180, 1959–1961. 1925.

In the experiments here described, tufts of the mosses were brought into the laboratory, and some were placed in closed glass vessels in a light-tight box while others were placed in similar vessels, but kept in the light near a window. The latter could, in some measure, be considered as a control regarding light effects. Examination of the cultures in the dark box was only carried out under extremely reduced illumination and at intervals of about one month. The small amount of light they received during such inspection was found to have no visible effect on the results.

The most noticeable effect produced by growth in darkness is a marked reduction in leaf size, so that the leaves no longer overlap each other on the axis. This effect makes an early appearance owing to the increased rate of growth of the axis which results under the experimental conditions, and it is accentuated by an increase in internodal length which these conditions produce.

Table I shows the relation between the average lengths of leaves on shoots grown in darkness, and on normal shoots for a number of different species. The former are indicated by the letter E, and the latter by the letter N. The third column in the table gives the values for the ratio N/E which expresses the degree of reduction in leaf length resulting from the experimental conditions. The first point of interest brought out by these figures is that the degree of reduction is much greater in the acrocarpous species than in the three pleurocarpous species examined, viz.: *Brachythecium rutabulum*, *Hypnum Schreberi*, and *H. cupressiforme*. Of these three pleurocarpous forms, *H. Schreberi*, which grows in nature usually under conditions of more intense illumination than the other two, shows the highest N/E value. A rather curious series is formed by the three species of *Mnium*. *M. punctatum* which is a very pronounced shade type shows the highest N/E value of the three; *M. undulatum* which is less of a shade type than *M. punctatum* but more so than *M. hornum*, has an N/E value

TABLE I

	E (mm.)	N (mm.)	N/E (mm.)
Brachythecium rutabulum	0·8	1·6	2·0
Hypnum Schreberi	0·4	2·1	5·25
H. cupressiforme	0·45	1·8	4·0
Mnium hornum	0·35	3·7	10·3
M. undulatum	0·35	7·5	21·5
M. punctatum	0·2	4·5	22·5
Dicranella heteromalla ...	0·09	4·0	44·5
D. squarrosa	0·3	3·2	10·3
Catharinea undulata ...	0·7	7·5	10·7
Dicranum scoparium ...	0·3	7·0	23·4

which is intermediate between those of the other two. On the other hand, in the case of the two species of *Dicranella*, *D. squarrosa*, which is an undoubted "sun" type, shows a much higher value than the shade type *D. heteromalla*.

This reduction in leaf size may be taken to be largely the effect of absence of light, as the leaves of mosses grown in glass vessels in the light showed only slight reduction in size as compared with normal leaves.

Regarding the form and size of the leaf cells, my observations confirm those of de Virville, viz. that there is a tendency for growth in darkness to produce a rectangular-elongate type of leaf cell. Where the cells of normal leaves are very elongated, growth in darkness reduces the elongation, and where the normal leaf cells are isodiametric, those of leaves grown in darkness are usually somewhat elongated. Cell differentiation in leaves disappears almost entirely in the case of plants grown in darkness, and is greatly reduced when plants are grown in light and moisture. In the case of plants grown under conditions of moisture-saturated atmosphere, cell walls were extremely thin irrespective of conditions of illumination.

The striking fact brought out by these experiments is that the experimental conditions, viz. high atmospheric humidity and darkness, tend to reduce the leaves of all mosses to one simple uniform type. See Figs. 1 and 2.

Most forms of leaf specialisation in mosses have been explained as adaptation to combat drought or to increase assimilation. From the point of view of experimental morphology, one might be led to suggest that the experimental conditions have here brought about some measure of reversion to a more primitive unspecialised leaf type. This point is particularly suggested by the effect of these conditions on species of *Fissidens* and *Polytrichum*. In both these genera we have normally a leaf structure that must be looked upon as specialisation in the direction of greater powers of photosynthesis and, perhaps, water retention.

Fig. 2 shows the leaf types produced by these plants grown in darkness and a moist atmosphere. In both cases, the specialisation of the normal leaves amounts to the production of an extra photosynthetic structure which has been added to the primitive leaf type and which in the case of *Polytrichum* is the elaborate leaf blade, bearing lamellae. The fact that these assimilatory structures are definite additions to the leaf types possessed by other mosses is strongly suggested by the fact that they disappear under the experi-
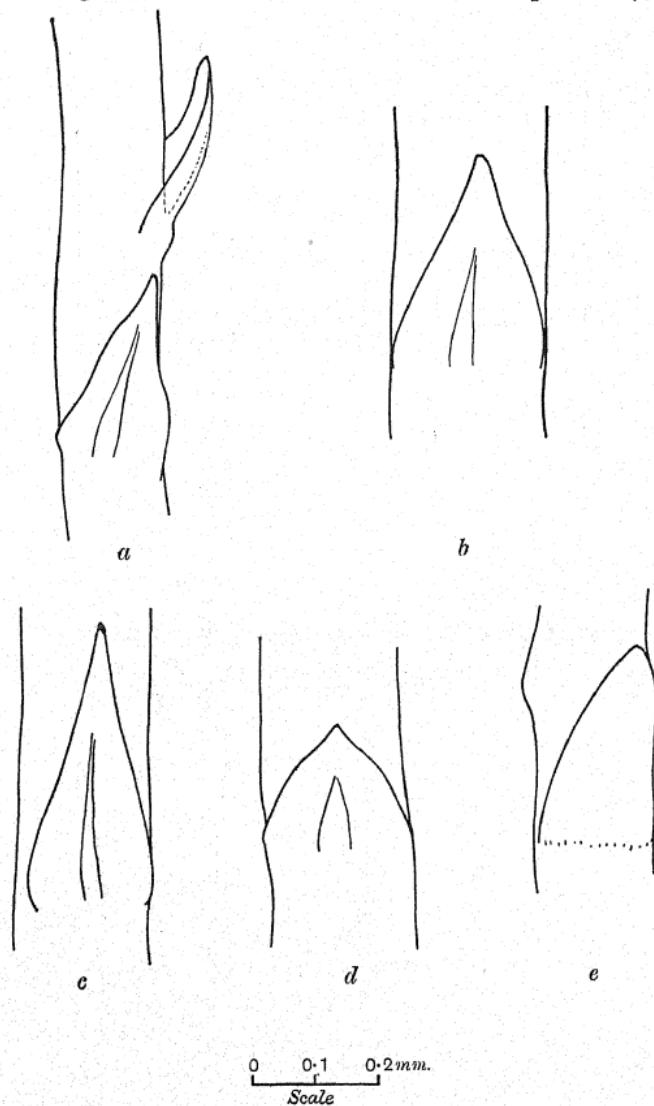
Fig. 1. Leaves developed on moss shoots grown in darkness and a moisture-saturated atmosphere. (a) *Dicranum scoparium;* (b) *Mnium undulatum;* (c) *Aulacomnium palustre;* (d) *Mnium punctatum;* (e) *Dicranella squarrosa.*
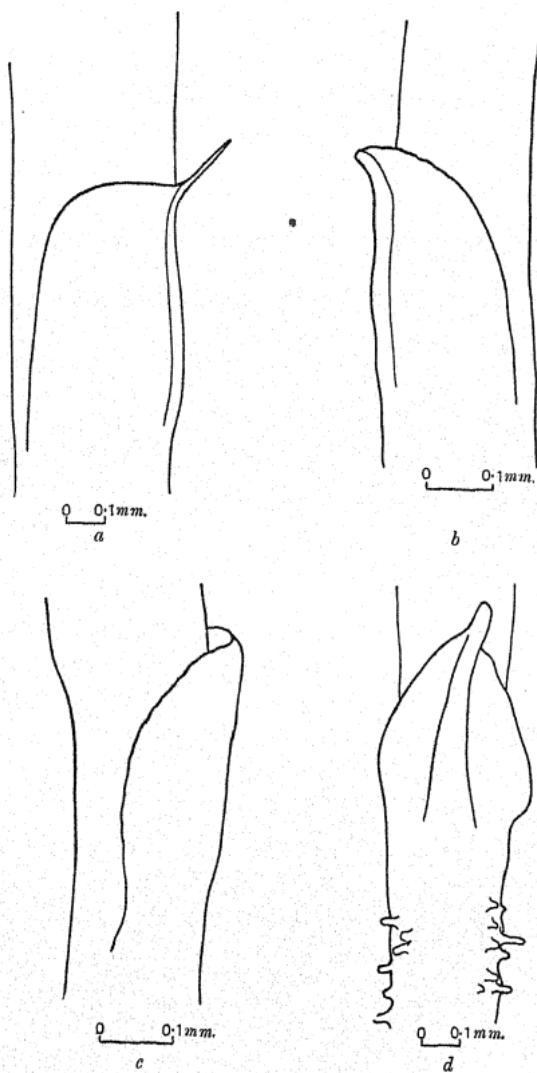
Fig. 2. Leaves of species of *Polytrichum* and *Fissidens* developed in darkness and a moisture-saturated atmosphere. (a) *Polytrichum commune*; (b) P. *juni-perinum*; (c) P. *aloides*; (d) *Fissidens osmundoides*.

mental conditions; leaving only reduced leaves comparable with those produced by other more typical species.

With regard to the effect of the experimental conditions upon stem structure, a number of observations and measurements were taken which will now be briefly described.

The number of leaves per centimetre on the shoots was determined in a number of species. The results of these determinations are given in Table II.

TABLE II

	N	ML	MD
Bartramia pomiformis ...	108	—	85
Brachythecium rutabulum	24	—	18
Catharinea undulata ...	26	15	14
Dicranum scoparium ...	44	18	18
D. majus	22	21	18
Fissidens osmundoides ...	20	—	18
Hypnum Schreberi ...	28	30	23
Mnium hornum	51	21	20
M. undulatum	17	—	13
M. punctatum	14	—	11
Polytrichum formosum ...	32	16	17
P. piliferum	70	25	20

N No. of leaves per cm. on shoots produced under natural conditions.
ML No. of leaves per cm. on shoots grown in glass vessels in laboratory in light.
MD No. of leaves per cm. on shoots grown in glass vessels in laboratory in darkness.

From these figures it will be seen that the experimental conditions result in increased length of internode. They also suggest that this increase is due to increased atmospheric moisture, and is not a true etiolation phenomenon.

The amount of growth that takes place in various species, when placed in darkness, varies between wide limits. In general it may be stated that more robust forms, such as species of *Polytrichum*, *Catharinea*, *Hypnum* and *Dicranum* will grow for weeks and, in some cases, months in total darkness, whereas small or delicate forms, i.e. species of *Anomodon, Tetraphis, Barbula* and small forms of *Fissidens*, do not grow at all. There seems reason to believe that the chief factor which determines whether a species will or will not grow in darkness is the amount of available stored food material present in its tissues. In the case of species like *Polytrichum juniperinum* and *P. piliferum*, which frequently colonise unstable sand, this ability to grow when covered, and thus deprived of light, is of great biological importance to them.

In addition to studying the effect of the experiments upon the length of internodes, measurements were made of the diameters of

moss stems grown in the field under normal conditions and grown in darkness as described. The numbers of cells across these stems as shown by median longitudinal sections were also counted. The results of these estimations are given in Table III. An examination of the N/E values for the stem diameters given in this table shows that, in every case but one, the experimental conditions resulted in a reduction in stem diameter. A further point of considerable interest is shown by the N/E values for the numbers of cells across these stems. It seems that the reduction in stem diameter produced by the experiments is due mainly to a corresponding reduction in the numbers of cells in the stems.

TABLE III

	Stem diameter in mm.			No. of cells across median longitudinal section of stem		
	E	N	N/E	E	N	N/E
Dicranum scoparium ...	0·20	0·41	2·05	13	26	2·00
D. majus	0·26	0·58	2·25	15	25	1·66
Hypnum Schreberi ...	0·41	0·60	1·46	26	34	1·30
Eurhynchium striatum	0·23	0·43	1·86	24	31	1·30
Thuidium tamariscinum	0·27	0·46	1·70	23	30	1·30
Mnium hornum	0·20	0·48	2·40	14	33	2·35
M. undulatum	0·59	0·54	0·92	22	25	1·14
M. punctatum	0·18	0·20	1·10	12	12	1·00
Philonotis fontana ...	0·16	0·39	2·45	12	25	2·10
Fissidens osmundoides	0·25	0·37	1·48	16	21	1·31
Bartramia pomiformis	0·14	0·32	2·28	12	26	2·16
Polytrichum formosum	0·33	0·58	1·76	28	48	1·72

   E Developed under experimental conditions in darkness.
   N Developed under normal conditions.

  An attempt was also made to determine if any general rule could be established concerning the relative sizes of the cells of the stems of mosses grown under natural conditions and under the experimental conditions in darkness. From these sections the average dimensions of cells from the middle cortical regions were obtained. The results of these measurements are shown graphically, and to scale, in Fig. 3.

  It will be seen that growth in darkness and moisture has a very varied effect on cell size in different species. One point, however, is of interest. It is suggested, by an examination of the cell diagrams (see Fig. 3) of the different species of *Dicranum*, *Mnium* and *Polytrichum*, that the experimental conditions tend to result in the production of a standard cell length for the different species of a given genus, and that this standard length may be arrived at by either a decrease or an increase.

  The marked differences between the cell diagrams (shown in Fig. 3)
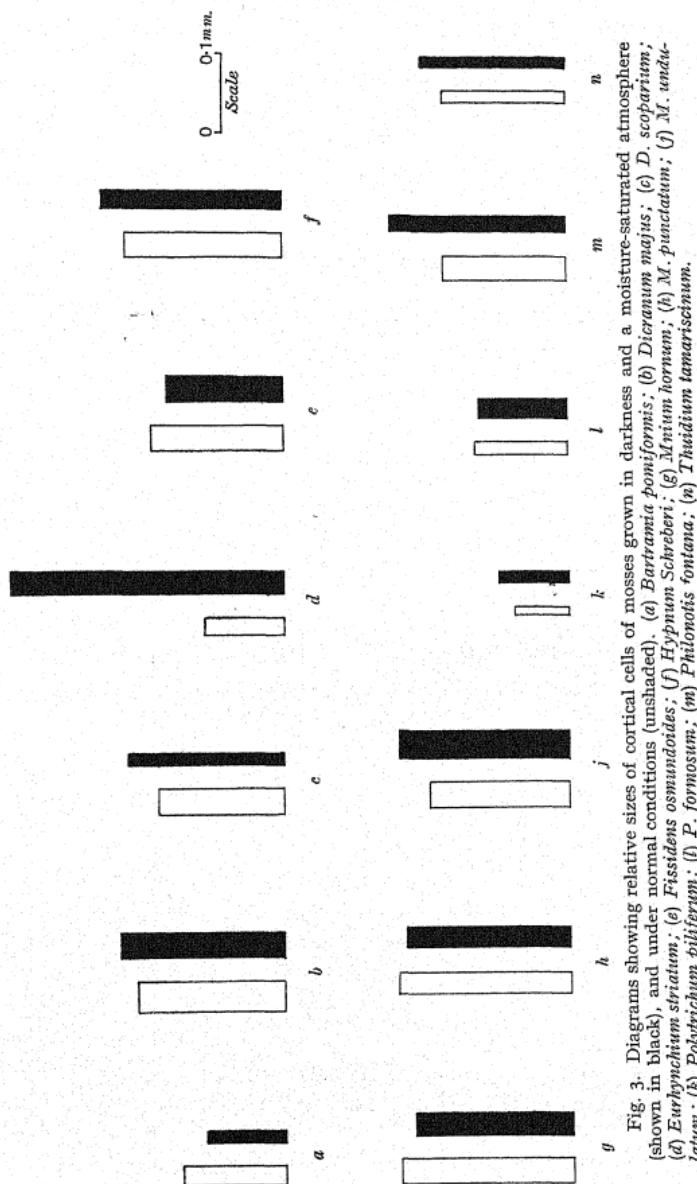
Fig. 3. Diagrams showing relative sizes of cortical cells of mosses grown in darkness and a moisture-saturated atmosphere (shown in black), and under normal conditions (unshaded). (a) *Bartramia pomiformis*; (b) *Dicranum majus*; (c) *D. scoparium*; (d) *Eurhynchium striatum*; (e) *Fissidens osmundoides*; (f) *Hypnum Schreberi*; (g) *Mnium hornum*; (h) *M. punctatum*; (f) *M. undulatum*; (k) *Polytrichum piliferum*; (l) *P. formosum*; (m) *Philonotis fontana*; (n) *Thuidium tamariscinum*.

for normal and for experimentally modified stems of *Polytrichum piliferum* and *Philonotis fontana* may possibly be connected with the fact that both species are "sun" types.

SUMMARY

    1. Modifications in the structure of certain mosses, brought about by growth in darkness and in a moisture-saturated atmosphere, are described.

    2. Leaves produced on shoots grown in darkness are much reduced in size.

    3. Pleurocarpous mosses show less reduction in leaf size than acrocarpous mosses.

    4. Differentiation of leaf cells is inhibited.

    5. Leaves tend to be reduced to a simple uniform type.

    6. The length of internodes is increased.

    7. The ability to grow in darkness varies widely with different species.

    8. Both the diameter, and the number of cells present in stems, are correspondingly reduced.

    9. There is a tendency for the experimental conditions to produce cortical cells of a standard length for different species of a single genus.

NOTE ON A SIMPLE GAS-CIRCULATING PUMP

By W. LEACH

(With 2 figures in the text)

I N the course of designing an apparatus for investigating certain
respiration problems, it was found that some form of pump was
required for the purpose of circulating the gas in the system. The
arrangement as described by Blackman and Bolas[1] was set up at
first, but, although it was quite satisfactory and efficient in its working,
it was felt that it would be an advantage if a pump of a more compact
form could be devised.

After some experimenting the apparatus shown in Fig. 1 was made
and was found to possess certain advantages over the Blackman and
Bolas type for our own particular purpose.

The pump was made of glass, and its construction should present
no difficulty to anyone moderately skilled in glass working. As will
be seen, the pump consists essentially of a U-tube containing mercury,
and having one arm considerably longer than the other. Connected
with the shorter arm B, which constitutes the barrel of the pump,
are two non-return valves of glass ground to glass seatings, and
arranged in the usual way to allow of circulation of gas through the
barrel in one direction only. These valves are made small in volume
and of a form which avoids as far as possible the presence of pockets
in which dead gas might hang.

Floating on the mercury in each arm of the U-tube are hollow
glass floats, slightly smaller in diameter than the bore of the arms so
that they move freely up and down as the level of the mercury
changes. The one in the pump barrel arm B has a rounded top, so that
when it moves upwards it displaces practically all the gas present
in B.

At the top of arm A is a side tube D, and a hollow, ground-in
stopper C. This stopper has ground to it a release valve G with a long
stem M which projects down below the rim of the stopper into the
arm A. Float K has a flat top so that, when it is raised, it comes into
contact with the valve stem M, and lifts the valve off its seating.

[1] *Annals of Botany*, **40**, 275. 1926.
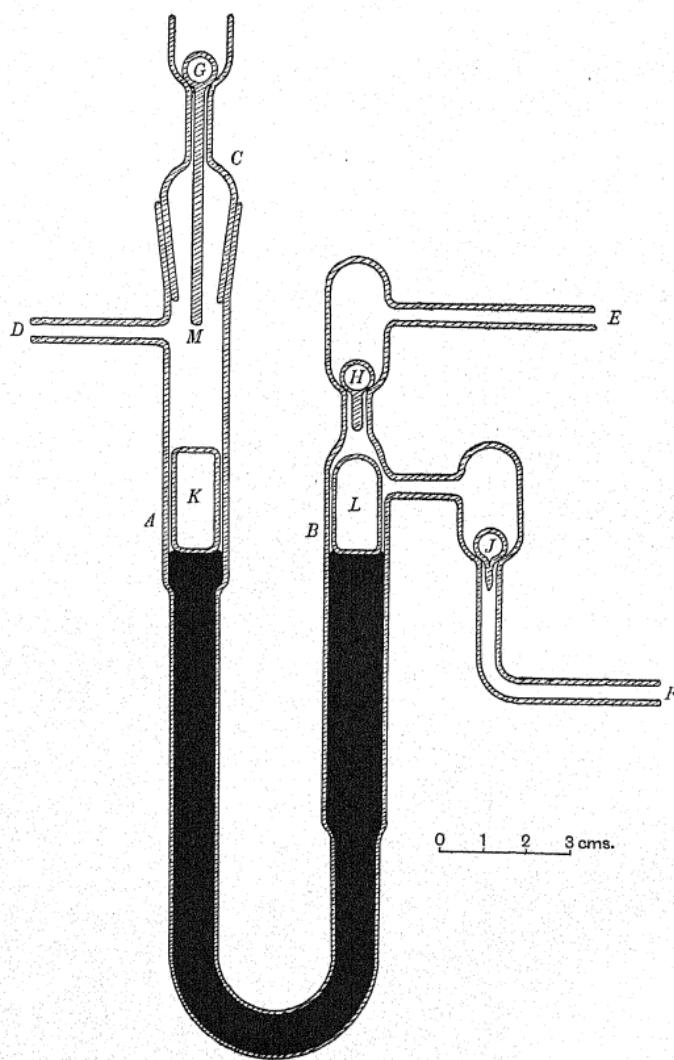
Fig. 1

Tube D is connected to an ordinary laboratory filter-pump as in the case of the Blackman-Bolas apparatus.

When the filter-pump is operating the mercury in arm A rises until the float K strikes the release-valve stem M and lifts it. Air then enters past G and the mercury falls, to rise again almost immediately as air is again removed from A by the filter-pump. This alternate rise and fall continues so long as the filter-pump is in operation. The up and down movement is transmitted to the mercury and float in arm B which results in gas being pumped round from F to E in the ordinary way.
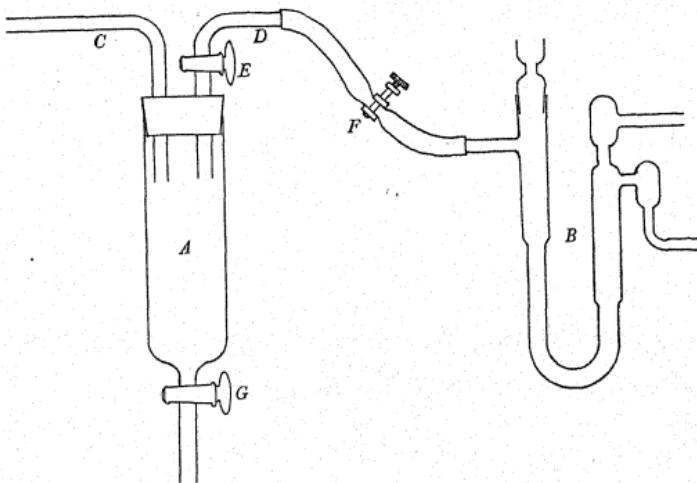
Fig. 2

The advantages claimed for this apparatus over the Blackman-Bolas type are as follows:

(1) Less mercury is required.

(2) No splashing of mercury occurs.

(3) There is less mercury in contact with the circulating gas.

(4) The volume of circulating gas in the pump is small.

(5) The action is more regular, the beats of the pump occurring at more frequent intervals.

(6) The pump is quiet in working, the only noise being that due to the opening and closing of the valves.

Although the pump shown in Fig. 1 is drawn to scale, its size and

proportions may be varied to suit any particular rate of gas circulation that is required.

The pump can be worked as described above, by simply connecting it to a filter-pump, the correct amount of suction for its operation being obtained by adjusting the water tap to which the filter-pump is attached. A more satisfactory method however is to fit it up as shown in Fig. 2. In this figure, the circulating pump B is shown connected by an india-rubber tube to a separating funnel A which is closed by a rubber bung. The separating funnel is connected to the filter-pump by means of the tube C. The air is removed from the separating funnel by the filter-pump, and the suction on the mercury in the circulating pump is adjusted by means of the screw-clip F. When this is done, and the circulating pump is working in its most satisfactory manner, it may be stopped and started again at will by simply turning the tap E off or on. The separating funnel also acts as a trap to catch any mercury that may be inadvertently sucked over when adjusting the clip F. This mercury can be drawn off by means of the tap G.

A WOUND SUBSTANCE RETARDING GROWTH IN ROOTS

By Sir FREDERICK KEEBLE, C.B.E., Sc.D., F.R.S.,
M. G. NELSON, M.A., AND R. SNOW, M.A.

(From the Department of Botany, Oxford)

I T has become well known through the experiments of Haberlandt and others (1, 3) that substances produced at the surfaces of wounds in plant tissues often increase the divisions of the underlying cells, and that these substances can be largely removed by washing. In the present note we report experiments which show, as we consider, another effect of wound substances removable by washing—namely, a retardation in the growth of decapitated roots.

Our experiments were performed on the main roots of young seedlings of *Zea Mays*, and of *Pisum sativum*, which were germinated in sawdust and kept both before and during the experiments in an electric thermostat at a constant temperature of 20° C. The plan was to compare the growth of roots which were decapitated and then washed for 15 or 30 minutes, with that of roots which were similarly decapitated but not washed afterwards. The latter were, however, always immersed in water *before* decapitation, for the same time and in the same conditions, in order that they might have an equal opportunity of absorbing water.

Since individual roots vary greatly in rate of growth, it is extremely important to select for comparison sets of roots that are as similar as possible. We, therefore, adopted the following method throughout. Large numbers of seedlings were grown, in batches of the same age, and the rates of growth of their roots were measured during a preliminary period of from 16 to 24 hours, or more often during two preliminary periods of about 7 and 18 hours. Pairs of seedlings were then selected which had grown at almost exactly the same rate during these periods, and were also of approximately the same length. The members of each pair were then separated into two sets, to be operated upon as experiments and controls. The method was laborious, and it also made it necessary to reject very many of the seedlings grown; but we found that it increased very greatly the consistency of the results. The underlying assumption was, naturally, that pairs of roots

that had been matched in this way were much more likely to continue growing at the same rate than pairs taken at random.

In order to wash the roots, we fixed the seedlings with their roots vertical by pinning the seeds to strips of cork at the bottom of glass vessels. The vessels were then kept filled with running tap-water, so that the entire seedlings were submerged. After the washing, the vessels were emptied of water, except for a shallow layer at the bottom, and were then closed with a lid, so that the seedlings were left with their roots in saturated air. If it was so required, they were easily rearranged with the roots horizontal. Strips of filter-paper were placed with one end submerged and the other end wrapped round the seeds, so as to supply water through them to the roots: for, as is well known, roots in damp air soon begin to slow down in growth, unless they are somehow kept supplied with water. With this arrangement, the roots grew rapidly and remained perfectly healthy for 48 hours.

In the four following tables we give the results of three different experiments with maize seedlings, and of one with peas. In each table there are included the results obtained with several separate series of seedlings, and the figures represent the mean growth of the decapitated and washed roots of each series after various times, expressed as a percentage of the growth of the decapitated but unwashed controls with which they were paired. The roots were washed for 15 minutes in running tap-water, except those of Series 5 of Table I and Series 1 of Table III, which were washed for 30 minutes in still water.

Expt. 1. (Table I.) *Zea Mays.* Growth of roots decapitated at 1 mm. from end of root-cap and washed, expressed as a percentage of the growth of similarly decapitated but unwashed roots that were paired with them. The roots were kept vertical.

TABLE I

	No. of pairs	Growth in first 5 to 6¼ hours	Next 15½ to 17 hours	Next 6¼ to 8 hours
Series 1	10	105·3	119·3	153·7
,, 2	7	125·0	106·4	103·3
,, 3	8	129·9	101·9	104·5
,, 4	12	159·2	104·6	141·3
,, 5	9	130·4	101·2	100·0
Total 46		Mean 131·5	106·9	123·7

Expt. 2. (Table II.) *Zea Mays.* This experiment was similar to Expt. 1, except that the roots were arranged horizontal. The results are expressed similarly.

TABLE II

	No. of pairs	Growth in first 5 to 7 hours	Next 16 to 17 hours	Next 6 to 7 hours
Series 1	10	126·0	121·0	100·0
,, 2	15	112·6	125·3	141·5
,, 3	11	78·8	102·1	—
,, 4	10	146·0	129·0	91·0
,, 5	6	150·0	119·7	113·2
	Total 52	Mean 118·7	119·6	114·9

Expt. 3. (Table III.) *Zea Mays.* As Expt. 1, except that the roots were decapitated at 0·5 mm. from end of root-cap. Results expressed similarly.

TABLE III

	No. of pairs	Growth in first 6 hours	Next 16 hours
Series 1	9	102	111
,, 2	18	91	135
,, 3	12	131	136
	Total 39	Mean 105·8	129·7

Expt. 4. (Table IV.) *Pisum sativum.* The roots were decapitated at 1 mm. from end of root-cap and arranged vertical, as in Expt. 1.

TABLE IV

	No. of pairs	Growth in first 5½ hours	Next 16½ hours	Next 6 to 8 hours
Series 1	15	110	110	96
,, 2	11	123	111	98
	Total 26	Mean 115·5	110·3	96·8

From the first three tables it can be seen that in all the 13 series of maize roots except one (Series 3 of Table II) the washed roots grew the faster on the whole, and further that in eight of the series they grew faster in every period of measurement. It does not appear that it made any difference to the results whether the pairs of roots were vertical or horizontal. Table IV shows that similar results were obtained with roots of *Pisum sativum* in the first two periods of measurement, though in the third period (after 22 hours) the washed roots fell slightly behind the controls in rate of growth. The results, when considered together, are so consistent that it seems certain that washing for 15 or 30 minutes did accelerate the growth of the de-capitated roots, and further that the effect lasted for 22 hours or more. We interpret this effect as showing that wound substances which

retard growth are produced at the cut surface of the root, and that these are largely removed by washing.

It might indeed be suggested that the washed roots grew faster because their cut surfaces enabled them to absorb more water than the controls, although the controls, as already stated, were immersed for the same time *before* decapitation. But since the root-cap, in *Zea Mays*, is about 0·5 mm. long, the cuts made in Expts. 1 and 2 at 1·0 mm. from the end must have passed only 0·5 mm. behind the vegetative apex, in a region where the differentiation of vascular tissue is only just beginning. Furthermore, in Expt. 3, the cuts were made at only 0·5 mm. from the end, and must therefore only just have grazed the vegetative apex. When therefore it is considered that all the seedlings, with the whole absorbing zones of their roots, were completely submerged during the period of washing, and also that afterwards water was continually supplied to the seeds in the manner already explained, it can hardly be supposed that the very small cut surfaces at the apices of the roots increased the absorption of water appreciably.

It seemed possible that the effect of wound substances on the rate of cell-division in the root might be different from their effect on growth, and that they might even accelerate cell-division, as they do in other organs. We, therefore, attempted to determine this point by noticing whether these substances affect the time taken by a decapitated root to regenerate a new tip. For this purpose, we decapitated roots of seedlings of *Vicia Faba*, but found that the time needed for regeneration of new tips was not appreciably altered either by washing the roots for 15 minutes on the one hand, or, on the other hand by covering their cut surfaces with a meal made by crushing several root-tips in a little water. We also found that roots of *Vicia Faba* regenerate new tips perfectly well, even when they are decapitated under water, transferred quickly to running tap-water, and then kept submerged in running water for the whole time.

It, therefore, appears that wound substances are not necessary for the regeneration of the root-tip, and there is so far no evidence that they even alter the rate at which it takes place. Němec had previously come on other grounds to a similar conclusion as to the effect of the wound ((2), p. 230). It is, however, quite possible that the wound substances derived from the root-tip may be found to accelerate cell-divisions in some of the other parts of the plant which have been found to be strongly affected in this way by their own wound substances.

SUMMARY

1. Roots of seedlings of *Zea Mays* and *Pisum sativum* that are decapitated and then washed for 15 or 30 minutes grow faster, during the next 22 hours or more, than similar decapitated roots that have been submerged for the same time *before* decapitation instead of after it.

2. It is concluded that substances retarding growth are formed at the wound, and that they are largely removed when the roots are washed afterwards.

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A NOTE ON THE OCCURRENCE OF A SMUT ON *SELAGINELLA CHRYSOCAULOS*

By T. C. N. SINGH

(With 5 figures in the text)

THE material on which this note is based was collected by Professor B. Sahni at Mussoorie (India) during October 1925 and was kindly placed at my disposal for investigation[1]. It was preserved in the field, in 4 per cent. formalin. The material was first thoroughly washed in running water (Ellis histological tank) for a full 24 hours to remove even the last traces of formalin. Then it was passed through graded series of alcohols to absolute alcohol. After this, embedding was done according to Dawson's method (1). Sections 6μ thick were cut and both double and single (safranin and iron-alum haematoxylin) stains were employed. The single stains, however, proved better than the double stains in bringing out the nuclei.

The occurrence of fungi on Lycopodiales is exceedingly rare. The only case which the author has been able to find in the literature is the occurrence of a Discomycete—*Acrospermum urceolatum* Olson on *Selaginella rupestris*—described by Miss Olson (2) in 1897.

In the case investigated the stems and leaves (usually the latter) of the diseased plants are covered with dark brown, sometimes black, irregular patches (Figs. 1, 2). An indiscriminate formation of such patches at almost any point on the plant seems quite common in *Entyloma* (3, 4). These dark brown patches are composed of resting spores which do not occur deep down in the tissue of the stem of the host, but in the leaf these spores do often occupy the whole thickness of the mesophyll. The spores are of varying size and shapes (oval, rectangular, triangular, ellipsoidal and circular) (Figs. 3–5). In most of the spores the walls are very much thickened, showing slight stratifications as in *Entyloma ranunculi* (5). The cell contents are brownish and granular with a pale translucent centre (Fig. 4 in the spore *A*). It is evident that the resting spores are mostly in an advanced stage of maturity. Mycelial hyphae are met with but very seldom. This is explained by the fact, that in the advanced stages *Entyloma* commonly produces resting spores on most parts of its mycelial hyphae (6).

Fig. 2

Fig. 3

Fig. 1

A
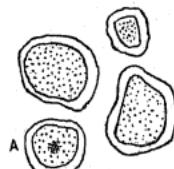
Fig. 4
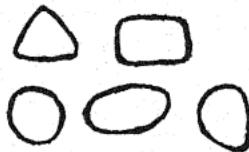
Fig. 5

Fig. 1. *Selaginella chrysocaulos*: a diseased shoot. × 1.

Fig. 2. *S. chrysocaulos*: a portion of the shoot magnified showing the black pustules. × 3.

Fig. 3. Young spores of *Entyloma polysporium* showing both the uni- and bi-nuclear stages. The top spore shows an early fusion uni-nuclear stage before the formation of the thick wall. × 550.

Fig. 4. Mature spores of *E. polysporium* showing the thick wall. In the spore marked *A* is represented the position of the pale transluscent centre by a loose black dot. × 665.

Fig. 5. Diagrammatic figures of the different forms of spores met with in the smut described.

In most mature cases the nuclei cannot be seen clearly because they are situated in the thick, brownish granular contents of the spores. Nevertheless, in young spores both the bi- as well as the uni-nuclear stages are visible (Fig. 3). This observation is in close agreement with the cytology worked out by Dangeard (7) and Lutman (8).

Unfortunately, the material available was inadequate for a study of the full life-history of this interesting smut. All that can be said is that the smut described closely resembles *Entyloma polysporium* (PK) Farl.

Finally I wish to express my sincere thanks to Professor B. Sahni, M.A., Sc.D. (Cantab), at whose suggestion this note was written and to Dr W. McRae, Imperial Mycologist, Pusa, for the identification.

INDORE CAMP, C.I. (INDIA).
    March 14th, 1930.

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THE

NEW PHYTOLOGIST

ROOT AND SHOOT IN THE ANGIOSPERMS: A STUDY OF MORPHOLOGICAL CATEGORIES[1]

By AGNES ARBER

(With 2 figures in the text)

CONTENTS

I. HISTORY OF THE CATEGORIES OF FORMAL MORPHOLOGY

THE impulse to analyse the plant into component members seems, in the first instance, to have arisen out of the desire to establish a comparison between construction in the animal and vegetable body; for the existence of a close analogy between the two was a fundamental postulate with the biologists of ancient Greece. The first extant attempt at such a morphological analysis is, in some respects, strikingly alien to modern botanical thought. It is that of Theophrastus (42), who, in the fourth century B.C., stated that "the primary and most important parts...are these—root, stem, branch, twig; these are the parts into which we might divide the plant, regarding them as members, corresponding to the members of animals: for each of these is distinct in character from the rest, and together they make up the whole." Theophrastus then proceeds to distinguish as subsidiary parts the leaf, flower, fruit, etc. He was influenced in this discrimination by the fact that in the tree, which he regards as the standard of plant life, the trunk and its branches persist permanently, whereas the leaf, flower and fruit are ephemeral. The importance of the leaf was destined to remain for long unrecognised, and it was not

[1] This paper forms part of the work carried out with the aid of a grant from the Dixon Fund of the University of London. An abstract of it was read at the International Botanical Congress, Cambridge, August 1930.

until Goethe[24] turned his attention to botany, more than two thousand years later, that the equivalence of the foliage leaves and the parts of the flower came fully to light[1]. But, inadequate as the botanical analysis of Theophrastus may seem to us now, certain of its features have shown remarkable endurance: these long-lived notions are the conception of root and stem as primary organs, and the idea of the leaf as something wholly distinct from the stem.

The discreteness of these categories—root, stem and leaf[2]—was reiterated by A. P. de Candolle[15] in the early nineteenth century, and it became the basis of the rigid morphology of the Sachsian era. In Sachs' *Text-book of Botany*[36] hairs are added as a fourth category; it does not seem worth while to spend time considering this wholly artificial addition, and I have ignored it in the discussion which occupies the later part of this paper. I do not suppose that any botanist would now be prepared to support the idea that the trichome constitutes a morphological unit of equal value with root, stem and leaf; indeed, since interest in morphology reawakened in the nineteenth century, the question has rather been whether even the three main categories can be maintained.

The earlier botanists were at least afflicted with no doubts as to whether the root was an important entity. They looked on plants primarily as the source of drugs, and the root was often the region to which they attached most value, and to which their attention was chiefly directed; the Greek herbalists were in consequence known as ῥιζοτόμοι, root-gatherers. But in more modern times, when botany began to free itself from the shackles of medicine, the root lost this extraneous interest, and, being out of sight, tended to slip out of mind. Goethe, for instance, practically ignores the root in his botanical philosophy[24]. And the majority of more modern writers have given little attention to the root, although they have generally adopted it *implicitly* as a morphological unit. Asa Gray[25] is an exception, for he suggested that the root was subsidiary to the stem. He took this view because he believed that the radicle was developed endogenously from the plumule; but for the Angiosperms this is certainly not true. Among the Pteridophytes, as Bower has shown[9], the main root is indeed lateral from the first, but this is not the case with the Flowering Plants, with which we are now alone concerned.

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[1] For an elaborate historical review of all the work on metamorphosis up to 1846, see Wigand[45].

[2] For references to a number of writers who have dealt with the morphological categories, but whose work is not considered here, see Chauveaud, *Ann. d. sci. nat.*, S. IX, 13, Bot., 1911, pp. 139 *et seq.*

In this group there is nothing in the ontogeny to conflict with the idea that the radicle of the embryo is a primary member, of equal importance with the plumule.

And if the position of the root as a morphological unit has not passed unchallenged, neither has that of the stem or the leaf; indeed, when we try to understand what has been thought of the status and relations of these two members, it is only too easy to get lost in a mist of controversy. One school maintains the view, connected with Gaudichaud's name[1] (21), that neither stem nor leaf is a valid category, but that the plant is formed of a series of individuals (phytons), each consisting of an internode with its upper node and the leaf there attached; a root, generally secondary, may be associated with the base of each phyton. In the words of Worsdell, who is an advocate of this view, "every stem is essentially built up of a sympodially developed succession of phyton units. The phyton is the true *Individual*" (46). Hochstetter (26), Delpino (19), Asa Gray (25), Čelakovský (17), Velenovský (44) and Chauveaud (18) have maintained views which are related more or less closely to those of Gaudichaud.

Another school of thought holds that the stem and leaf are independent categories, but that the true stem is a mere core, and that it is entirely enveloped by a cortex derived from the leaf-bases. This pericaulome theory, though foreshadowed by Hofmeister (27, 28), was first fully expounded by Potonié (33), who was led to it by his study of fossil Cryptogams. The leaf-skin theory of E. R. Saunders (37) seems to be in essence an extension of the pericaulome idea to the Flowering Plants; this author concludes that the "surface tissue of the Spermophyte shoot axis is of foliar origin." But, unlike Potonié, she does not commit herself to an opinion about the nature of the tissues underlying that superficial component—undefined in depth—which she distinguishes as "skin."

A third theory, that of Lignier (31), will be discussed at a later point, since it is more fitly considered under the head of evolutionary than of formal morphology.

Considering that almost all botanists are concerned to some degree with the Flowering Plants, it is surprising that so few have expressed a clear idea of any kind about the relations of stem and leaf. In modern textbooks one generally finds that the writers are content to drop the clean-cut Sachsian units, without substituting anything else for them. Or if the subject, instead of being simply shelved, is submitted to discussion, it is apt to lead to such a despairing conclusion

[1] For a history of this view see Velenovský (44), pp. 550–1.

as that of Kerner [29], who writes that "the whole matter finally ends in an unfruitful strife of words where everyone is in the right."

II. DISCUSSION

In the preceding paragraphs a few of the main standpoints of formal morphology have been surveyed rapidly and without criticism. We must now try to make a closer analysis of the plant body, in order to evaluate for ourselves the various morphological categories which have been proposed; and then attempt to bring these concepts of formal morphology into relation with those of evolutionary morphology.

(i) *Stem and leaf in formal morphology*

We have shown that the idea of a morphological distinction between stem and leaf was originally suggested by the deciduous character of foliage. But leaf-detachment often occurs at a level which obviously cannot be taken to coincide with a morphological boundary. Many such erratic instances might be cited, but it will suffice here to recall one example from among the Gramineae; in the Bamboo, *Arundinaria falcata*, Nees, the disarticulation occurs *above* the base of the leaf-sheath, which is left as a collaret surrounding the axis [22]. But if the simple plan of taking the absciss layer to mark the limit between stem and leaf is inadmissible, where are we to set this limit? Alexander Braun [10], nearly eighty years ago, wrote of the "essential interconnection" of these two organs, and since his time no one has succeeded in satisfactorily delimiting them. Casimir de Candolle suggested [16] that the morphological unit was not the leaf but *leaf + leaf-base + leaf-trace*. This formula may seem hopeful at first glance, but its application leads one inextricably into difficulties. Consider the broad-based leaves of *Zea Mays*, L., and *Saccharum officinarum*, L., which are supplied by numerous leaf-traces; the median bundle may descend for six internodes in Maize and about eight internodes in Sugar-cane before it attaches itself to the shoot system, while in the minor bundles such unions take place progressively earlier in the downward passage—the smaller bundles only remaining free for one internode or even less [40, 8]. If the boundary between leaf and axis is to be determined by the traces, where are we to set it in such plants as these?

Nor is any settlement of the problem achieved by those who adopt the pericaulome or related theories. These writers are clear about the *outer* limit of the leaf tissue, which on their view coincides with the

entire shoot surface, but they offer no clue which will help us to dis-
cover the *inner* limit which separates the foliar tissues from that
central region to which they confine the term "stem." Others, such
as Delpino(19), avoid the problem of boundaries by the simple ex-
pedient of dethroning the stem altogether. They take from it even
its last stronghold, the axial core, and regard the region commonly
called the stem as consisting merely of fused leaf-bases. On the
opposite side, certain botanists, instead of treating the whole ex-
ternal surface as foliar, are prepared to allot to the stem various
regions commonly attributed to the leaf. Hochstetter(26) and
Bugnon(13), for instance, treat the so-called leaf-sheath of Grasses as
a local transformation of the stem. The close relation of leaf-base and
axis in this family is shown by the fact, to which Lehmann(30) has
drawn attention, that the Grass pulvinus may consist exclusively of
leaf-sheath tissue (*Poa pratensis*, L.) or almost exclusively of haulm
tissue (Bambuseae), or it may be formed from both (*Zea Mays*, L.).

Among structures outside the Gramineae whose axial or foliar
nature is still in dispute, may be mentioned the tube of a gamope-
talous corolla, and the outer region of the wall of an inferior ovary.

We may conclude from this survey that no unanimity has ever
been reached on the question of exactly what regions of the plant
body are to be attributed respectively to stem and leaf. And even
when we study members about whose stem or leaf nature there is
no dispute, we frequently find that the characters which are supposed
to differentiate these two entities prove, on close scrutiny, to be
invalid. There are many such instances in the literature, but I will
not now cite them, since I should prefer to draw my illustrations
from my own observations, and chiefly from the Grasses, a group
with which I happen to have been working. I have little doubt that
corresponding cases would be found in any family which one studied
intensively. Space only allows of a brief summary of the points in
the structure of Grasses which have a bearing on the vexed question
of the relation of stem and leaf: figures and further details will be
found in my papers ((2), etc.).

One of the postulates of formal morphology is that a leaf cannot
be terminal to a stem. We know that beside the base of the uppermost
leaf borne by any axis there is generally to be found an apical cone,
interpreted as consisting of axial tissue, and thus representing the axis
to which this uppermost leaf is lateral. In the Monocotyledons this
cone is sometimes reduced to very small dimensions. I have figured
sections of the shoot-tip of *Uvularia* showing extreme reduction

of this apical cone ((1), Fig. xxxv, p. 58). But in certain Bamboos
in which I have examined the spikelet structure by means of serial
sections, I have found that the entire apex of the spikelet axis is
regularly transformed into a leaf (a flowering glume); *no trace* of
apical tissue is left over, so there is no axis to which this uppermost
leaf can be interpreted as lateral[1]. I recorded this for *Gigantochloa
Scortechinii*, Gamble, and *Oxytenanthera nigrociliata*, Munro, in a paper
published in 1926(2) and described it more fully in 1928(4). Since
these papers appeared, I have confirmed the observation for *Giganto-
chloa Scortechinii* in material from another source, and I have also
found a corresponding terminal leaf in *Oxytenanthera auriculata*, Prain,
Gigantochloa Kurzii, Gamble, and *Schizostachyum Hasskarlianum*,
Kurz. The behaviour of these five species, representing three genera,
shows that it is not inherently impossible for an axis to terminate
in a leaf. In a recent paper(39), E. R. Saunders writes—in reference
to certain cases which she holds to be somewhat analogous to that of
the Bamboos just considered: "Though a truly terminal position for
a normal foliar member is contrary to the fundamental relation of
stem and leaf, it is nevertheless the case, where extreme reduction
brings the axis ostensibly to vanishing point, that a reduced leaf
member may be formed which has all the appearance of being actually
terminal." But in the spikelet of *Gigantochloa* and the other Bamboos
described, the entire shoot apex forms the leaf, so that the axis is
not only "ostensibly" but *in reality* brought to vanishing point, and
the leaf member not only "has all the appearance" of being terminal,
but actually *is* so. Surely we must recognise that facts are still facts,
even when they have the misfortune to conflict with the canons of
morphology.

Another dictum of formal morphology is that the power of pro-
ducing lateral shoots is confined to axes. When a leaf does, in fact,
bear a shoot-bud, this shoot is called "adventitious," which means
literally "accidental." This is a typical example of the tyranny
exercised by words over thought; just because they have themselves
labelled these buds "accidental," botanists feel justified in dismissing
them as of no morphological significance. But there are certain in-
stances in which leaves produce shoots with such precision and regu-
larity that we can scarcely shut our eyes to their behaviour, however
inconvenient it may be from the point of view of the rigid demarca-

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[1] As will be recognised from this description, E. R. Saunders is incorrect
when she cites my observations as referring to "the imperfect spikelet...re
duced simply to the flowering glume" ((38), p. 574).

tion of stem and leaf. "Nepaul Barley" is a case in point((6), pp. 520–7, Figs. 5, 6, 7). In this strange form (*Hordeum trifurcatum*, Jacq.) the bract in whose axil the flower arises (known in the Grasses as the lemma or flowering glume), produces accessory spikelets from near the apex of its upper (ventral) surface. This peculiarity is not casual or sporadic, but is heritable, and definitely characterises the race. Those to whom the canons of morphology are sacred, explain these accessory spikelets as buds whose position is really axillary to the flowering glume, but which have been carried up on its surface to a distance from their actual point of origin. But detailed study lends no support to this view. The orientation of the one-flowered accessory spikelet is always the same—its palea backs on to the ventral surface of the flowering glume, and its rachilla lies between the two; this is not what we should expect if the glume were the axillant leaf. There is not, moreover, the slightest anatomical indication that the glume below the origin of an accessory spikelet consists of axillant leaf and bud fused together; on the contrary, the accessory spikelets receive their vascular supply direct from the simple collateral strand which forms the median bundle of the glume. We can but conclude that the flowering glume, which is a *leaf* member, behaves to the accessory spikelet in all respects as if it were that spikelet's parent *axis*. And so we return—as we so often must—to the standpoint of Goethe, whose morphological insight long ago led him to recognise "The fertility which lies hidden in a leaf" ((24), § 76).

Another example of a leaf that manifests, though on different lines, an axis-like behaviour, may be taken from a family so remote from the Grasses as the Ranunculaceae. The leaf of *Thalictrum* is much subdivided, and in certain species at the base of each segment an appendage is developed which, *if it occurred in association with the base of a complete leaf*, would undoubtedly be classed as stipular[1]. In this respect the leaf segments of each order treat the rachis from which they spring as if that rachis were their parent axis. A leaf of *Thalictrum aquilegifolium*, L., showing stipular collars of four orders, C_1–C_4, is drawn in Fig. 1; the collars are seen in section in B_1 and B_3. It is interesting that Casimir de Candolle was struck by the axis-like symmetry of the petiole of this species(16). It thus provides an exception, on the part of the leaf, to the generalisation that the structure

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[1] Velenovský calls these appendages "Nebenblättchen oder Stipellen"(44) and Goebel also names them "Stipellen"(23), but the use of this term cannot be maintained if we accept Casimir de Candolle's definition of stipels(16) as organs developed on the *adaxial* face of the leaf, for the outgrowths in question are chiefly *abaxial*.
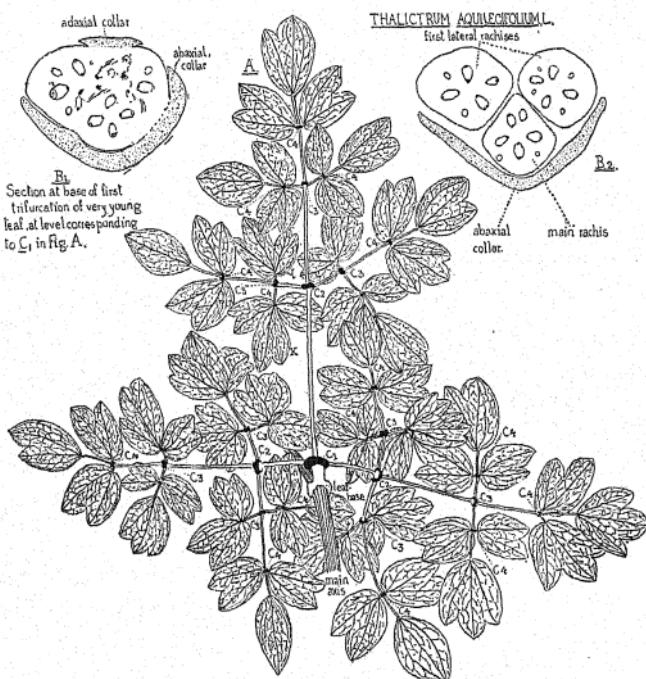
Fig. 1. *Thalictrum aquilegifolium*, L. A. Abaxial view of foliage leaf ($\times \frac{1}{3}$ circa);
stipular collars indicated in black; main axis ribbed; two axillary branches
omitted. The leaf drawn consists of a leaf-sheath and very short petiole, at
the top of which there is a trifurcation, and the first stipular collar, C_1. Each
of the three branches behaves alike. Each trifurcates again at C_2, with a
collar at the level of trifurcation, and each of the nine branches thus
produced trifurcates twice, at C_3 and C_4; each branch terminates in a leaflet,
and there are no collars of a higher order than C_4. The trifurcation at C_4
may be incomplete (e.g. at X), or there may be no collar, and still less sign
of trifurcation (e.g. at Y). In other words, the leaflets of each final trio may
be imperfectly separated, but wherever the terminal leaflet is discrete and
petioled, there is a collar at the trifurcation below it. B_1, B_2. Transverse
sections ($\times 31$ circa) through the first trifurcation of a young leaf at
a level corresponding to C_1 in A. The stipular frill or collar is a non-vascular,
cup-like structure; the larger collars consist of an adaxial as well as an
abaxial member; the abaxial member is bifid. The smaller collars are
reduced to the abaxial member alone.

of the stem conforms to radial symmetry, while that of the leaf is symmetrical about the antero-posterior plane only. And on the part of the stem, striking exceptions are found among Grass inflorescences. For instance, the branches of the first order in the inflorescence of *Luziola Spruceana*, Benth. ((5), Fig. 1, B_2, p. 392; Fig. 3, A, p. 397; Fig. 4, C_3, p. 399) and the rachillae of *Arthrostylidium longiflorum*, Munro ((7), Fig. 4, B, p. 771), show an imperfect dorsiventral symmetry, which affects the arrangement of both fibres and vascular strands. In the plan of their skeletal system these axes recall certain petioles. The same tendency to dorsiventrality may also be traced in other axes which are less richly vascular. In the Hordeums, for instance, the inflorescence axis is liable to be strongly dorsiventral. The bundles may be arranged in a flattened ellipse with two main strands situated at the foci, e.g. *H. jubatum*, L. ((6), Fig. 2, A_1, p. 510). Or instead of an ellipse there may be a single row of bundles as in *H. pratense*, Huds. ((6), Fig. 2, B_8, p. 510); any anatomist who was shown an isolated section of an internode of the inflorescence axis in this species, might well suppose that he was looking at a foliar member.

As an example from outside the Gramineae illustrating the loss of radial symmetry in an axial member, I may cite the pedicels of the Cruciferae, which are frequently dorsiventral in anatomy and recall petioles in their ground plan. To illustrate this point I have drawn sections of the inflorescence axis and pedicels of *Rapistrum Linnaeanum*, Boiss. et Reut. (Fig. 2, A_1–A_3, p. 307).

Loss of radial symmetry is particularly noticeable in those Grass shoots which show extreme reduction in anatomy. The fertile spikelets of *Cynosurus cristatus*, L., the Crested Dog's-tail Grass, are accompanied by sterile spikelets—delicate pectinate objects, at first glance suggesting a pinnate leaf. But more careful examination shows them each to be a complete shoot, consisting of an axis bearing a number of distichous leaves. The vascular system of this shoot is reduced to the lowest possible limit. The axial region is traversed by a single collateral bundle, which gives off leaf-traces to either side ((4), p. 176, Fig. 1, E, F, p. 175). And among the Grasses, such extreme vascular reduction is by no means confined to sterile spikelets. I have met with species in which the stalk of a fertile one-flowered spikelet is supplied by means of a single collateral bundle alone, e.g. both male and female spikelets of *Luziola Spruceana*, Benth. ((5), Fig. 3, I_2, p. 397; Fig. 4, C_8, p. 399) and hermaphrodite spikelets of *Alopecurus pratensis*, L. A rachilla, moreover, may be one-bundled even when

it is destined to bear more than one flower. In sections of certain small spikelets of *Poa annua*, L., I found that there was only one collateral vascular bundle in the region between the first and second flowers of the spikelet. The rachilla produced a second normal flower laterally, and also continued beyond this flower, producing another abortive flower, above which it died out. So here, we have a one-bundled dorsiventral axis capable of still further development even after producing an axillant leaf (lemma) and lateral shoot (flower).

One-bundled rachillae, when seen in transverse section, may exactly simulate the awns of the glumes, which are always treated as leaf members. This is shown for *Lamarckia aurea*, Moench., in (4), Fig. 3, cf. F_1 and F_2, p. 179. A one-bundled rachilla in association with the palea of the flower which it bears (e.g. *Hordeum distichum*, L., var. *nigrum*, (6), Fig. 4, B, p. 517), may closely resemble an awn with the bikeeled glume to which it belongs (e.g. *Anthoxanthemum odoratum*, L., (3), Fig. 1, A_7, p. 475, glume 4, with its awn). Such comparisons obviously cannot be pressed far, but they at least show that structures which rigid morphology regards as purely foliar, can, on occasion, develop on much the same lines as structures in which the axis is held to play a part. But however this may be, there is no doubt that a rachilla whose vascular system is reduced to a single collateral bundle has, by the loss of radial and the retention of dorsiventral symmetry, become foliar rather than axial in the character of its anatomy.

Its radial symmetry is not the only distinguishing feature which the axis may lose. It may also forfeit its anatomical predominance in relation to the leaf. This happens, for instance, in the abortive lateral spikelets of *Hordeum distichum*, L., var. *nigrum* ((6), p. 516, and Fig. 3, B–D, p. 515). These spikelets consist of an axis bearing two or three small leaves, equivalent to the glumes of the fertile spikelets. Two or three bundles enter the base of the minute shoot, but when they are followed up, they all prove to be leaf-traces for the first glume. A bundle for the continuation of the axis is given off from the median bundle of this glume, or even from one of its lateral bundles. In the latter case it would be strictly in accordance with the facts to speak of the vascular supply for the upper region of the axis as given off from a minor bundle of a leaf; but such a description would be an infringement of the conventional canons of morphology. *Thalictrum aquilegifolium*, L., furnishes a corresponding example from outside the Grasses, though here we are concerned with well-developed and highly vascular organs. The large complex foliage leaf,
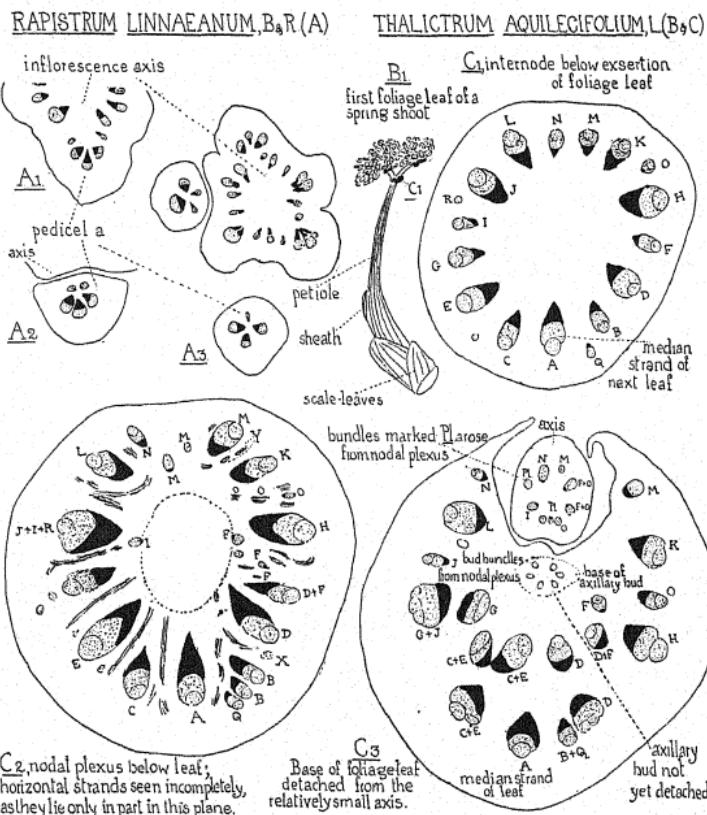
Fig. 2, A_1–A_3. *Rapistrum Linnaeanum*, Boiss. et Reut. Transverse sections from below upwards to show the origin of pedicel *a* from the inflorescence axis ($\times$ 47). A_1. Part of the inflorescence axis; the five bundles to the south enter the pedicel *a*. A_2. Pedicel *a* detached from the axis. A_3. Axis and pedicels at a higher level; the two smaller bundles in *a* have fused into one. B, C. *Thalictrum aquilegifolium*, L. Tip of shoot to show apparently terminal leaf as it first appears above ground in the spring (March 20th); C_1, stipular collar of the first order (nat. size). C_1–C_3. Transverse sections through the exsertion of the very young uppermost foliage leaf of a shoot ($\times$ 23). The lettering is arbitrary and is merely intended to make it possible to follow the history of the bundles. C_1. Internode below leaf. C_2. Partial view of plexus beneath leaf exsertion. C_3. Base of leaf with the bundles for the axillary bud, which is at this level unconnected with the small axis.

to which we have already referred (p. 303 and Fig. 1, p. 304), alto-
gether overpowers the shoot-apex to which it is technically said to
be lateral; the analysis of the vascular relations of these two members
shows that the leaf is in reality, and not merely in appearance, the
predominant partner. This is illustrated in Fig. 2, B and C, p. 307;
in C_1–C_3 the bundles are lettered so that their history can be followed.
C_1 shows the internode below the uppermost leaf; there is a ring of
bundles. In C_2 a nodal complex has arisen, partly by branching of
the members of the bundle ring, but partly through the appearance
of new meristematic tissue in the intervals between the strands;
X and Y are examples of the latter type of origin. In C_3 the large
leaf-base is seen detached from the small axis, which is supplied by
minor branches from certain leaf bundles and from the nodal plexus.
Anatomically the shoot-apex is thus a mere appendage of the vascular
system of the leaf.

In these examples from *Hordeum* and *Thalictrum*, it is the leaf
that usurps the status of the axis. But the converse may also occur.
In Grass inflorescences there is a strong tendency to leaflessness, and,
in correlation with this, we find examples in which leaf-traces are
replaced by branch-traces which take a longitudinal course. In
Grasses attention was first drawn to this feature by Bugnon (11), who
observed it in *Poa annua*, L. I have since illustrated it for *Dactylis
glomerata*, L., where it happens to reveal itself diagrammatically
((5), Fig. 5, p. 401).

Further instances might be cited[1], but those which I have brought
forward are perhaps sufficient to show that "leaf" and "stem" are
liable to adopt one another's characters in a disconcertingly protean
way. Attempts to formulate their differentiating features lead us
into the same confusion as those attempts to delimit their respective
spheres which we have already discussed. There must surely be some
explanation for the fact that as soon as botanists try to arrive at any
clear understanding of the relation of stem and leaf (considered as
discrete morphological entities) they find themselves involved in a
welter of contradictory opinions. Is not the explanation merely this—
that *the problem itself is imaginary?* For the bitterest controversies
always rage round problems which cannot be solved for the simple
reason that their very existence is an illusion. If we once accept the
fact that "stem" and "leaf" are no more than convenient descriptive
terms, which should not be placed in antithesis as if they corre-

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[1] E.g. the history of the rachilla in *Bromus mollis*, L., and *Cephalostachyum
virgatum*, Kurz, which is summarised from this point of view in (3), p. 486.

sponded to sharply opposed morphological categories, the problems
of their delimitation and of their differentiating characters vanish
into thin air.

(ii) *Shoot and root in formal morphology*

A study of the relation of the so-called axial and foliar members
in the plant body has led us to the negative conclusion that stem
and leaf cannot be accepted as valid morphological categories. This
conclusion involves the rejection of Potonié's "Pericaulom" and
"Urcaulom" as fundamental units, since they imply an absolute dis-
tinction between axial and foliar parts[33]. But if we discard stem
and leaf, what units are we to adopt? For the leaf-bearing region
of the plant two alternative unit categories (not postulating a mor-
phological distinction between stem and leaf) have been suggested
at different times:

      (1) The phyton.
      (2) The individual shoot (primary or lateral).

The phyton theory seems to me to belong to that group of over-
ingenious, academic conceptions which are difficult to discuss because
they bear so little relation to reality[1]. The phyton theory has indeed
a certain superficial simplicity, but it becomes excessively compli-
cated as soon as it is applied to different types of flowering plants.
In the shoot of a Monocotyledon with sheathing leaf-bases, the
phytons or "Sprossglieder" are described as *superposed*, so that each
internode belongs to one morphological unit. In a shoot, however,
which bears whorled or spirally placed leaves whose attachments are
relatively narrow, each "stem segment," as Čelakovský points out[17],
must be regarded as built up of as many *juxtaposed* units as there
are orthostichies. This means that in general the internode of a
Monocotyledon consists of a single morphological unit, while that of
a Dicotyledon consists of a complex of such units. A theory which
needs so much manipulation before it will fit the facts of plant life
is an invitation to scepticism.

I am not overlooking the fact that Priestley, in a recent suggestive
study of the development of the flowering plant, has shown that the
"Sprossglieder" of Čelakovský[17] correspond to units of growth[35].
It seems to me, indeed, entirely natural that an individual leaf, and
the part of the axis served by the trace which passes into this leaf,

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[1] For a criticism of Chauveaud's version of the phyton theory[18], see
Bugnon[12].

should be closely related in their growth-history; but I do not see how any morphological conclusion can be drawn from this relation.

The idea of the shoot as a unit is much older than the idea of the phyton. Goethe[24] was so much absorbed by the consideration of the leaf and its metamorphoses that he paid scant attention to the rest of the plant body, but yet it is to him that we owe the first really lucid statement as to the importance of the individual shoot. He related lateral buds to seedlings, and regarded them as individual plantlets comparable with the parent shoot. The same idea was emphasised later by Alexander Braun[10]; as evidence for the individuality of the shoot rather than the leaf, he pointed to the products of root-budding, which are always adventitious shoots and not individual leaves. In more recent days Bower[9] has stressed the importance of "the simple shoot" as a vegetative unit.

I think that Goethe had seized the right clue when he singled out the shoot for special attention, but his notion remained incomplete because he seems to have forgotten the root. If one accepts the shoot as a unit, the body of the flowering plant must be held to consist of parts belonging to two categories only—*root* and *shoot*. The point I wish to emphasise—which, obvious as it seems, does not appear to have been made before—is that these two entities are strictly comparable in the vital matter of reproduction. Each normally gives rise to other units *like itself*, and to nothing else; the shoot produces lateral shoots which are a repetition of the parent shoot, while the root produces lateral roots which are similarly a repetition of the parent root. The essential identity of lateral roots with their parent root seems to me to invalidate Potonié's suggestion that they are related to the parent root as leaves are related to the axis[33]. Lateral shoots and roots are parallel, not only in being repetitions of the parent organ, but also in showing an analogy in their position of origin, which seems in both cases to be determined by anatomical factors.

That shoots and roots, superficially dissimilar as they are, yet have a fundamental correspondence, is revealed by the fact that shoots can give rise to roots, and that roots, though more rarely, may produce shoot-buds. This suggests that in both shoot and root the potentiality of the other unit lies dormant beneath the character which predominates. Moreover, the cotyledons may be claimed as indicators of the essential unity of shoot and root, since they show that the root is not entirely devoid of the power to produce leaves. For the hypocotyl—the "axis" on which the cotyledons are borne— is often internally more root-like than shoot-like, and the anatomy

of the cotyledons themselves is apt to retain hints of root structure. The remarkable external differences so often met with between the cotyledons and later leaves may well be due to the fact that the cotyledons take their origin from a region which retains root characters, whereas the later leaves are derived from a region which is purely shoot[1].

The striking differences in form between shoot and root originate out of the fact that—in addition to the uniform apical growth which both members share—the shoot has a second growth rhythm, localised both in longitude and latitude, which gives rise to outgrowths (leaves). We should be beginning to understand the differences between shoot and root if we could explain why the shoot shows this *localised and rhythmic cell multiplication* in the superficial tissues, while in the root the tendency of the outer elements is not so much towards cell division as towards that mode of *increase of surface area of individual cells* which produces the root hairs.

(iii) *Formal and evolutionary categories*

Up to this point I have considered morphological categories in the light of pure or formal morphology alone. I have done this deliberately, because I think that these categories ought to be evaluated quite apart from the doctrine of descent. Morphology existed long before it received an evolutionary explanation: more than two thousand years ago Aristotle had grasped the homology between the forefeet of quadrupeds and the hands of man, though for him it had no evolutionary implication[32]. The next stage in our argument must be to discover how far the results at which we have arrived through the study of formal morphology are consistent with the findings of evolutionary morphology.

Our conclusion that shoot and root are primary and equivalent categories has already led us to discard one of the theories which claim to represent the historical course of evolution—the phyton theory. This theory was founded on the study of the living plant, and it cannot be said to have received any support from palaeobotany, or from general considerations about the course of evolution; there is thus no need to reconsider it at this point.

The pericaulome theory of Potonié[33], which we have also rejected on grounds of formal morphology, is in a somewhat different position, since it claims support from the historical evidence of fossil

[1] See the discussion on seedlings in (1), p. 177, etc.

botany. It is difficult to attach any meaning to this theory unless one can believe that at some historical stage the leaf-bases possessed downward prolongations which were at first free from the axis, but which subsequently fused with it, and with each other, to form an enclosing rind. But in the case of the Angiosperms, with which we are now alone concerned, there is no historical evidence that such a process has ever occurred; and nothing even remotely suggesting it takes place in the course of ontogeny. It is indeed true, as Čelakovský pointed out in 1901[17], and as E. R. Saunders has more recently demonstrated in detail[37], that the surface of the Spermophyte shoot is in many cases[1] mapped out into areas each of which is associated with a leaf; but this is a perfectly natural result of the mode of growth, and in no way implies an actual clothing of the shoot with foliar tissue. Each leaf rudiment in a young shoot represents the growth focus of a certain area of shoot surface, and it is interesting, but not really surprising, that these areas continue to be traceable even at maturity, when the great elongation to which the stem is subject has altogether altered their proportions. Saunders speaks of the leaf rudiments as "fused along their contiguous margins." This seems to be an artificial way of visualising the facts; in reality no such fusion occurs in the development of the young shoot, nor does the leaf show "the downward extension of its tissue" which she postulates. We may conclude, I think, that the evidence against the pericaulome theory, considered as a description of an evolutionary process, confirms our rejection of it on grounds of formal morphology.

There is yet a further theory of the history of the plant body in the Spermophytes, due primarily to Octave Lignier[31], though other botanists, before or since, have in part foreshadowed it, or applied it in special directions[2]. It may be summarised in the briefest possible fashion as follows. The primaeval vascular plant is visualised as a cauloid, with no distinction of shoot and root. This cauloid—in the phylum which eventually gave rise to the Angiosperms—became differentiated into a subterranean region (root) and an aerial region. The aerial cauloid then suffered a reciprocal differentiation into what we now call stem and leaf, the leaf being merely a specialised cauloid

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[1] For exceptions see Bugnon[14], and Arber[3], pp. 485-6. I formerly[1] accepted the leaf-skin theory, but further work has now convinced me that it is untenable; the element of truth which it contains is merged in the conception of the shoot as a unit.

[2] On the higher plants see especially Casimir de Candolle[16], who treats the leaf as a branch with its posterior face atrophied, and also Dingler[20]. Much of the most important work on the subject relates to the Ferns, and is thus outside the scope of the present paper; see Tansley[41].

branch of limited growth. This idea of the essential equivalence of
stem and leaf has recently received striking confirmation from the
work of Uittien (43), who has shown that among the Flowering Plants
there is a correlation between the relative lengths of the main and
lateral axes of the branch system, and of the main and lateral nerves
of the leaf. The theory of Lignier is simpler than the phyton theory
or the pericaulome theory, and it can be applied without strain to a
variety of cases. Moreover, it is not inconsistent with such palaeo-
botanical evidence as is available. It seems to me that it deserves
to be accepted as more probable than the other alternatives sug-
gested, but with the reservation that any such theory is in its very
nature so speculative that it ought not to be treated as anything
more than a provisional working hypothesis.

It is noticeable that two morphological conclusions are implicit
in Lignier's theory: firstly that, if one thinks back to origins, no
fundamental distinction exists between stem and leaf, and secondly,
that root and shoot are wholly equivalent entities. But these two
results are just those at which we had arrived independently from
a consideration of formal morphology alone; that they are consistent
with that theory of evolutionary morphology which appears most
securely based, adds to the probability that they represent at least
an approximation to the truth.

III. Summary

The various views which have been held regarding the morpho-
logical units which make up the plant body in the Angiosperms are
first briefly summarised. The question of the relation of the aerial
axis to its appendages is then analysed, and it is concluded that *stem*
and *leaf* should not be treated as discrete morphological entities.
After a further discussion of the plant body as a whole, the result is
reached that *root* and *shoot* belong to primary and equivalent morpho-
logical categories. Up to this point the discussion has been limited
to formal or pure morphology. The plant body is next considered
from the somewhat different standpoint of evolutionary morphology,
and it is concluded that, of the alternative theories offered, Lignier's
idea of the differentiation of a primitive cauloid is probably of most
value as a working hypothesis, though its speculative character is
fully recognised. But the morphological principles deducible from
Lignier's theory are just those to which the study of formal mor-
phology has been shown to lead—the equivalence of root and shoot,

and the absence of a real morphological distinction between stem
and leaf. The fact that these conclusions have been reached inde-
pendently both from the formal and from the historical standpoint,
increases the probability that they are valid.

CAMBRIDGE.
    May 31*st*, 1930.

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STUDIES IN THE PHYSIOLOGY OF CAMBIAL ACTIVITY

III. THE SEASONAL ACTIVITY OF THE CAMBIUM

By J. H. PRIESTLEY

(With 1 figure in the text)

CONTENTS

INTRODUCTION

I T was originally intended to devote this paper to certain detailed observations upon cambial activity throughout the season, prefaced by a brief analysis of earlier statements upon the same subject. When, however, the literature was re-examined in the light of experience gained during the detailed examination of a few species, the impression steadily strengthened that, instead of being, as is usually supposed, a mass of conflicting or discordant data, the earlier statements present a very consistent picture of the essentials of seasonal cambium activity, especially in the case of the hard-wood tree. For the moment, therefore, the presentation of the Leeds observations is deferred in order to permit of a more thorough examination of the literature than was originally intended. Whilst, as a result, citations of earlier work are fairly numerous, they are by no means complete, some forestry papers in particular being inaccessible to the writer. Many observations also are not discussed because they only describe the radial growth at certain positions on the trunk.

The resumption of cambial activity in each growing season is a

somewhat elusive phenomenon: beginning in one region it gradually spreads to others and, similarly, its fluctuations and cessations of activity are not simultaneous throughout the whole of the tree. Observations confined to a few points on the tree may, therefore, give a very inaccurate impression of the real nature of the rhythm of this growth activity. Fortunately the picture can be completed with the aid of many observations in the earlier literature, and as a result a definite impression emerges as to the nature of this process which is very suggestive in relation to other physiological activities of the tree.

These pages are devoted, therefore, to building up such a comprehensive picture of the general progress of cambial activity in the tree throughout the season. Such a general statement should provide an incentive to the detailed and laborious accumulation of data which alone can control its accuracy.

The results of such detailed observations upon *Acer Pseudo-platanus*, and upon certain soft-wood species, will be presented in separate papers. The experience gained during their accumulation has been of great value in preparing the present paper and the data gathered are in general accord with the account of seasonal cambial activity which is given below. Other such detailed surveys of some English trees are projected because, as will appear in later pages, certain trees may possess characteristics of cambial activity or of differentiation of the secondary tissues derived from the cambium, which mark them out as particularly interesting from the present standpoint. The story of seasonal cambial activity, however, will remain very incomplete till data are available for all types of climate in which trees grow, and it is hoped that this general statement of the problem may draw investigators into this field who may have facilities to study trees in widely differing habitats.

In the woody perennial, both apical growing points and inter-calary meristems may be active from year to year, and in the English climate such activity, for obvious reasons, is seasonal in nature. An English or north European observer may thus easily be led to attach too much importance to features of this rhythmic growth activity which are the immediate result of the somewhat extreme changes of temperature which accompany the seasonal changes in these countries. But the evergreen tree in such a tropical locality as Buitenzorg, where all seasons are not only warm but also wet, still shows indications of an internal rhythm of growth, although now that the *tempo* is less strictly prescribed by external conditions, which are never such

as to prevent growth of some kind proceeding, this internal rhythm is irregular, not only when one tree is compared with another, but in the phases of the growth cycle exhibited at the same time by different branches of the same tree (Coster(8)).

These considerations have led most observers to conclude that this internal rhythm of growth in the plant is autonomic and not aitiogenic, but in the early part of the present century a very lively controversy was in progress upon this question, to which access can be readily obtained through such general résumés as those of Kniep(39), Lakon(50) and Klebs(37), or through the papers of Kühn, Simon, Weber, etc. (36, 46, 49, 78, 79, 86, 88, 90).

Stimulated perhaps by the success obtained by Johannsen(32) in the practical process of forcing the resting foliage and flower buds by ether vapour, a number of methods were devised which showed the great part that external conditions played in the maintenance of the dormant, winter condition of the tree(88). Klebs, in particular, used great experimental ingenuity in showing that, not only could dormant buds be brought back to an active growing condition, but that, by a suitable manipulation of external conditions it was possible to keep the shoot of the tree in an active condition of growth for a very long period and, in some cases, continuously throughout the year(36, 37). The beech (*Fagus sylvatica*) had proved a peculiarly intractable plant but finally, by growing a seedling tree in a pot in a greenhouse, with the illumination of a 1000 candle-power Osram lamp, Klebs succeeded in keeping this shoot in active growth. He concluded that, provided external conditions were suitable, the shoot growing point could be maintained in a state of active growth and that any existing rhythm must be aitiogenic in character.

Klebs' conclusion as to the possibility of maintaining the plant apex in vegetative growth activity might be valid, and yet the *natural* rhythm of the plant would still remain the result of the interaction of internal, autonomic and, to some extent, inherited factors with the changing external conditions. Thus, Klebs himself is led to attribute importance to the excessive piling up of organic metabolites as a factor contributing to the normal entry of the buds into the dormant stage; the *relative* lack of inorganic salts in comparison was regarded as a contributing factor, and the subsequent renewal of active growth in many cases was attributed to the arrival at the growing centre of more inorganic salts. Lakon supplied further experimental data in support of this influence of nutrient inorganic salts on the renewal of growth in buds upon cut shoots(49, 50), but

the later experiments of Kühn (46) suggest that Klebs and Lakon may have over-estimated the significance of inorganic salts.

The experimental possibility of maintaining a growing apex in continued vegetative activity does not diminish the significance of the existence of a natural rhythm of growth which must finally be traced to a fluctuating rhythm in the essential conditions for growth, provided for the meristems by complex internal systems. This will be equally true for an intercalary cambial zone as for an apical meristem. If, therefore, when seasonal changes in the tree are regarded from a wider angle, the general significance of the direct effect of climate is minimised, an increasing significance appears to attach to the correlations between such growth activities as extension growth of shoot and root and the radial increase of that part of the axis which has ceased to extend in length. In the present study of the seasonal activity of the cambium, therefore, it would be unwise to neglect other seasonal growth activities of the tree.

In a sense, the perennial is a plant which has obtained a degree of release from the obligate rhythmic succession of vegetative phase, reproductive phase, somatic death and seed dispersal, which, in the life cycle of a trivial, is a rhythm already relatively independent of season. This release the perennial owes to some internal mechanism which checks the swing from vegetative to reproductive growth activities before it takes too big proportions, so that continued somatic vegetative activity remains compatible with flower and seed production. None the less, the same rhythmic change still manifests itself in such a plant, and, following the pioneer work of Klebs, the pomologist has learnt to follow it in the changes in the carbohydrate/nitrogen ratio (29). Thus, a period of vigorous vegetative growth and leaf production with low carbohydrate reserves is followed by carbohydrate accumulation, flower and seed production, but this involves carbohydrate expenditure, and thus a return to the earlier vegetative phase. This internal rhythmic cycle is a complex process, of which the physiology, morphology and anatomy are alike equally obscure.

At the shoot growing point leaf initials, bud scales and flower primordia (Foster (14)) may follow one another, as the result of meristematic activities which are governed by very complex correlations, associated with metabolic supplies and with other factors affecting growth. The rhythm of cataphyll and foliage leaf production by the growing point takes place in the vegetative shoot apex without overstepping those limits of growth activity which are associated with vegetative growth. With a wider change in the conditions of growth

at the apex these meristematic activities alter more fundamentally and the shoot apex produces flower primordia instead. From bud scale to leaf production is a growth rhythm which is usually seen each year in every vegetative bud, but a wider change is involved in the conversion of a shoot apex to a flower bud. Such changes affect usually only a proportion of the buds on the plant in any one year and in some trees cycles of flower bud production are liable to occur only at intervals of years.

In some of the fruit trees there is very considerable evidence of a bi-annual rhythm of "bearing" and "off" years and correlations have already revealed themselves to the pomologist between such internal rhythms of vegetative and reproductive growth activity and metabolic storage balances, indicated by the carbohydrate/nitrogen ratio, and also such growth activities as the relative amount of extension and radial growth (Finch [13]).

In discussing the seasonal activity of the cambium, therefore, it is essential to remember that this is a meristem of which the cells have potentialities of growth very exactly equivalent to those possessed by the cells of the apical meristem in the same plant. Even the present preliminary survey of the seasonal activities of the cambium will show how intimately they are connected with the activities of the apical meristem and there is little doubt that with a more adequate knowledge of these different growth activities their close inter-relation will only be emphasised.

It is convenient to commence our present study with the awakening of the cambium to activity in the spring. Throughout the winter in North America and northern Europe, where most cambial studies have so far been carried out, the above-ground portions of the tree are almost at a standstill so far as growth is concerned. Jost [35] and Küster [48] have reported some growth activities in the buds throughout the winter, as Askermasy had done earlier; Simon [78] has shown that quite a vigorous respiratory activity is maintained through this season.

The outward manifestations of such growth activities are slight, but there are many evidences that changes must be proceeding. Thus in the autumn, in many trees, the buds are dormant, that is they fail to develop when brought into warm, moist conditions in the laboratory. But if the same buds are given the same conditions later in the winter, they promptly develop, showing that this condition of dormancy has disappeared. The curious disappearance and reappearance of starch which takes place in the phloem during the winter

(Swarbrick[83, 84]) is another indication that changes are still proceeding: in fact, in the phloem in particular, it is not at all clear that there is any marked cessation of the activities of growth and differentiation during the winter. The point will be referred to again later.

These relatively subordinate activities in the stem in winter are probably related to changes still in progress, below ground, which are still far too little known. Long ago von Mohl[60] described root activity in some trees as lasting well into the winter. He saw the oak roots continuing growth until February, the ash until March and the apple and cherry until April. Russow[74] and Th. Hartig[26] subsequently decided that the conditions during von Mohl's observations were exceptional, but Harris has since reported[20], even for the cold winter climate of Oregon, continued growth of roots throughout the winter provided they were not killed by immersion in standing water. These continued growth activities of the root, at least so long as the soil is not frost-bound, must mean the continued activity of osmotic systems in this region of the tree[76, 77]; these will be responsible for the gradual rise of the water table in the wood which is so conspicuous a feature of all observations upon the conditions of the wood throughout the winter months (Craib[9, 10], Farmer[12], etc.). This growth process must also be associated with the removal of food supplies from the older roots, a process which is recorded by Wotchal[89], and here it probably links up with the autumn activity in phloem production in the tree which will be discussed later in this paper. At the moment we get an impression of relative quiescence in the above-ground portion of the tree, associated with a certain amount of growth activity below ground, thus driving water into the main mass of the wood throughout the tree and so gradually preparing for the great burst of growth activity which is shown by the tree in the spring.

THE COMMENCEMENT OF CAMBIAL ACTIVITY IN THE SPRING

The winter and spring state of the cambium

Before any cell divisions appear in the cambial layer in the spring, a very marked difference is shown in its appearance. Swarbrick states that at Long Ashton in the apple he observed a swelling of the buds, accompanied, or followed almost immediately, by a swelling of the cambial tissue over the whole tree above ground[83]. The cambium became swollen, turgid and translucent in appearance as contrasted with its somewhat shrunken, opaque appearance during

the winter. The contents of the cambium cell then became much less densely granular and far more difficult to see in microscopic examination of the unstained tissue. The cambium at this time, throughout all the axis in which wood has been laid down in previous years, is a relatively narrow belt of tissue immediately on the face of the fully lignified wood formed in the previous season. The walls of these cells are relatively thick and, as the cell contents swell at this stage, it appears that their nature changes materially (82, 83). The writer suggests that these changes are in accordance with a resumption of the sol state by the bulk of the protoplasmic contents of the meristematic cells which, at the commencement of the winter, parted with a certain amount of water and went into a gel state in which condition they were relatively resistant to frost.

It is with the resumption of the sol state by the cell contents that this layer of cells with relatively plastic walls, and now semi-fluid contents, once more comes into a state well-known to the practical forester and horticulturalist, who describes it by stating that the bark will now "slip" upon the wood so that the two can easily be separated along the plane of the cambium. Before the tissues resumed this semi-fluid condition, which is a necessary prelude to their growth activity, the bark would not "slip" in this characteristic manner over the wood.

The resumption of this semi-fluid state by the meristematic layer is a fairly rapid process and is conditioned by external circumstances, especially temperature. It is probably also associated with the gradual filling of the wood with water during the winter and the displacement of air from the intercellular spaces in the rays in the neighbourhood of the cambium. The relative suddenness, however, with which the change takes place all through the aerial portion of the tree (very little is known about the roots in this connection, but the bark certainly "slips" here also in the spring) suggests that the determining factor is a change in the relation of the protein contents of the cambium cells to this surrounding water, a change which waits upon the external temperature, etc., and which occurs fairly suddenly throughout the whole cambial layer. Following this change, Swarbrick noticed starch disappearance occurring in the phloem and in the cells of the cortex progressively outwards from the phloem, but for fourteen days or so after the cambium has thus resumed its active growing condition no cell divisions have been noticed in it and he observed no starch disappearance on the side of the xylem. The radial increase in dimensions resulting from this swelling may be quite

appreciable. Professor B. T. P. Barker has drawn my attention, at Long Ashton, near Bristol, to the early and sudden swelling of the trunk of a tree which takes place in March or even in February, and which may cause a wire circlet, which could be moved freely up and down the tree at one time, to be firmly held and cutting into the bark twenty-four hours later. This swelling of the trunk may thus be of considerable practical importance in connection with such restricting bands, which require careful watching at this time of the year. It takes place many days before any new cells are cut off by the cambium in the same region of the trunk. For whilst this swelling of the cambium and resumption of its normal, plastic, semi-fluid nature takes place throughout the tree at practically the same time, cell division in the cambium begins later and usually is very local indeed in its first occurrence. This point admits of ready observation, and yet so little attention has been paid to it that the literature is full of contradictory statements about the region where cambial activity recommences, most of them made on very incomplete evidence. It is necessary to submit this literature to a little analysis because it would appear from its superficial study that no regular rule applied to the initiation of cell division in the cambium. This is thought to be the reverse of the truth. So far as the writer is able to judge, incomplete and scattered observations have obscured the emergence of a most important generalisation as to the initiation of renewed cambial activity in the buds which will prove fundamental to a proper understanding of the process of cambial growth and its physiological consequences.

Two methods of attack upon this problem are possible: (1) direct field observations upon cambial activity in different parts of the trunk, and (2) experiments designed to analyse the possible connection of such renewal of cambial activity with food reserves, leaves, buds, etc. Both such types of observation are upon record and will be considered. For the purpose of precision the data will be analysed separately for hard-wood and soft-wood trees, although such treatment may necessitate a certain amount of repetition. The point which proves to be at issue is whether the cambial activity begins indifferently anywhere or at different places in different trees, or whether the normal method of resumption is first in the buds and from thence down to the trunk and roots in a basipetal manner. The data will therefore be analysed from this standpoint. A very useful résumé of many of the data discussed will be found in a paper by Grossenbacher [16].

The initiation of cell division in the cambium in the Dicotyledon

In the Dicotyledon, although a recent and very valuable text-book contains a quite contrary generalisation ((11), *loc. cit.* p. 155), there is really very little doubt that cambial activity in the spring normally begins in every active bud as it resumes growth. The first resumption of cambial divisions on the axis, where the cambium has been present through the winter on the face of the wood of a previous year, will be found to occur just below the point of insertion of such a bud. Actually this observation means that cambial activity is initiated in the bud, and probably at the base of a young leaf initial, where, as already pointed out ((64), *loc. cit.* p. 14) the first tangential longitudinal division in the procambial strand may precede all xylem differentiation and all the xylem subsequently differentiated may take its origin from what are, in this sense, secondary tissues (Kostyt-schew (43, 44)). Just as xylem differentiation proceeded basipetally from this position, so cambial activity continues basipetally down the elongating internode. The meristematic activities connected with various foliar strands may thus link up in the procambial strand of the young shoot and, at its base, these cambial elements are in con-tinuity with the cambium layer of the leaf traces subtending the bud and thus with the cambium of the main axis as a whole. Thus, after cambial activity begins *in* the bud, it gradually spreads downwards into the axis, being usually particularly prominent where it faces upon xylem that is in direct continuity with the xylem of the foliar strands of the leaf that originally subtended the bud. This cambial activity is not only found on the main axis just below the terminal bud, but it is also to be seen below every other bud in the shoot which is commencing growth. As a result the axis of the tree, when cambial activity commences, is covered with little wedges of new tissue, spreading relatively rapidly downwards and slowly horizon-tally around the stem, formed from the separate renewal of activity beneath each bud. This observation was made originally by Th. Hartig in 1862 (24) when studying the behaviour of willow cuttings; Simon (70) makes it again in 1914. Hartig also noted that this activity spread only basipetally from the base of each bud and that even if the cutting was inverted, the cambial activity still spread in the same proximal direction. It is undoubtedly here that the solution is to be found of the curious behaviour of inverted pieces of stem in graft unions. Rothe found it very difficult to get such inverted pieces of stem to make unions at all, it was only possible to get the distal end

of the inverted piece, now nearest to the stock, to make a successful union with the cut stump of the stock by making this union several days before the other proximal end of the inverted piece was given an opportunity of forming a union with the base of the scion (72). In such inverted pieces, excessive cambial activity takes place at the upper (proximal) end of the inverted piece, whilst the lower, distal end shows very little cambial activity, and therefore very ineffective union with the stock below. In this, as in nearly every other case where the progress of cambial activity has been studied, there are no records of an upward movement of cambial activity from the bud in a distal direction. Almost the only case where such upward transmission of cambial activity has been seen in stems has been in hardwood cuttings, which had been made when the cambium was dormant (Sledge (80)). In these stems cambial activity began at the base as the result of the wound and from thence spread gradually up the stem as well as, in time, downwards from the buds when they began to push. This observation was also made by Hartig in 1862, but appears in have attracted very little attention. Jost (33, 35) also noted the close connection frequently to be seen between bud development and the subsequent basipetal spread of cambial activity. He was particularly concerned with the problem of the relation of cambial activity to food reserves and showed in many ways that this type of meristematic activity was far more intimately connected with bud development than with food supplies. Thus, if woody shoots were placed in the dark, if the buds developed, cambial activity could be traced working downwards on the woody stems in regions beneath such etiolated sprouts and nowhere else. In this case no general cambial activity over the whole axis supervened, and the strict localisation of this new cell division in the cambium to the regions immediately below developing etiolated shoots was very evident. Jost also observed cases where, after extension growth had ceased in the summer and the cambium had been forming summer wood with thick walls, the premature forcing of the buds which would normally have remained quiescent through the winter, but which instead grew out into "Johannistriebe" or "lammas shoots," was sometimes followed by a new crop of thin-walled wood of the spring type, so that, for a certain distance down the shoot, two "annual" rings of wood were formed in the one growing season.

Whilst the observations so far cited have mainly been made on deciduous trees, the work of Reiche in Chili (71) and more recently of Coster in Java (8) makes it equally clear that in the evergreen, also,

the cambium usually has quiescent periods and that its renewed activity commences with the outgrowth of the axillary buds. Cambial activity may then resume in the leaves, as also in such evergreen leaves when taken off the plant and struck as cuttings, and Jost regards such leaves as the most striking example known to him of cambial activity that is independent of the presence of lateral growing organs situated on the same axis, above the place in which the cambial activity is manifested.

Strasburger also states that cambial activity in the Dicotyledons usually commences at the base of the new shoot and spreads from there basipetally downwards on the trunk(81). He does not appear, however, to have made a very close analysis of the early distribution of cambial activity and it is not possible to attach any significance to certain exceptions he cites from the Leguminoseae as the details supplied are not sufficiently explicit. Thus, in *Robinia Pseudacacia* on April 30th the cambium had started in the main trunk as well as the twigs, but the buds had only just begun to grow out. In *Gleditschia horridus* on April 30th the buds were still closed, but the cambium was active in the main shaft and twigs. In *Cercis siliquastrum* no cambial activity was visible in the second-year shoots when the leaves of the new shoots were already one-third their full size.

R. Hartig had previously pointed out that, in the copper-beech, in which the periderm layer is thin, the cambium seems to become active throughout the trunk at practically the same time if the tree is growing in an open situation(21, 22). On the other hand, if the tree is in the shade, cambium activity at the base may lag very considerably. Lodewick again(51, 52) has concluded that in certain Dicotyledons, especially in the ring-porous species, cambial division may begin independently in the trunk, but in his observations no special attention was paid to the region just below the buds, and all these somewhat indefinite observations, which suggest but do not prove a separate start of cambial activity in the main trunk and branches, which *might* be independent of buds, are no longer critical enough to establish a point which has become of very great importance.

Chalk(5), from observations made near Oxford, stated that in the common ash, *Fraxinus excelsior* L., growth had started in the stem 2 weeks before it started in the twigs. From the paper, it would appear that this observation was incidental, most attention being paid to the radial increase in girth of the trunk throughout the year. We have noticed at Leeds that, in the ash, the radial growth of the

trunk makes a surprising amount of progress at a time when the buds, as a whole, show very little development. Several factors may play a part in this process; in the first place, the vessels on the older part of the sub-aerial axis develop to a relatively enormous size very rapidly; secondly, the cambium is of the stratified type in which, possibly, cambial activity propagates relatively rapidly in a tangential as well as a vertical direction. At Leeds the buds upon the lower branches of the ash, and also adventitious buds directly on the trunk, push much earlier than the buds on the upper part of the tree, and whilst it is possible to find higher branches in which radial growth has not commenced whilst the trunk already shows activity, so far no tree has been observed showing cambial activity in the trunk without any signs of cambium activity on some of the branches. Furthermore, the branches show the usual obligate connections between the bud and cambial activity. In no case is cambial activity found in these twigs which is unconnected with the bud above and when the bud fails to grow the cambium below fails to become active unless other buds are present and active in more distal positions. This cambial activity on the first- and second-year shoots is not so conspicuous because the vessels are smaller. Probably, however, the relation of cambial activity to the buds in *Fraxinus* is most obscured by the fact that the early development of flower buds initiates cambial activity and xylem differentiation on both branches and main trunks. A superficial examination, before the leaf buds break and after the flowers have fallen, may thus easily lead to the conclusion that cambial activity is not associated with the buds.

In the light of these facts, Chalk's statement that he found cambial activity proceeding in the trunk for a fortnight before it started in the branches has little significance when no data are given as to the method of sampling the trees under examination. We are told that these trees were growing in an open position so that the buds and cambium upon the lower branches would probably be active at an earlier date than the buds and cambium of the more apical branches, and in such trees places would be found on the branches where cambial activity had not started although started in the trunk, but none the less the cambium activity in the trunk would probably still depend upon the lower buds on the lower branches on the trunk.

For similar reasons the modifications in this basipetal propagation of the inception of cambial activity stated by Mer (56, 57) cannot be evaluated without much more precise data as to his method of

sampling than are given in his papers. Mer apparently happened to
choose for examination only species in which cambial activity begins
under the apical buds, a rule which is broken by the ash as we have
just seen. With young trees, in close stands, he found a basipetal
propagation of the activity; in older trees, in open situations, whilst
the apical activity was still first, he found such an early cambial
activity at the swollen bases of some of the branches and in the swollen
basal portion of the trunk that he suspected an independent origin
of cambial activity here which may also persist in these same regions
for an unusually long period, thus accounting for the unusual girth
at these points. In view of the discussion of Chalk's more recent
results with ash, it is clear that these observations require re-
examination, with a special reference to the possible local activity
of low growing branches and adventitious buds situated on the trunk
itself, in the case of trees growing in such open situations.

The observations of Swarbrick at Long Ashton(83,84) and of
Knight and his colleagues at East Malling(40) in which cambial
activity in fruit trees has been followed in detail, once more establish
the existence of a basipetal impetus to cell division which commences
in the buds; the East Malling observations, incidentally, have com-
pletely explained the significance of the "feather," the name given
to the crop of small lateral shoots upon the main branches, which is
due to the influence of these lateral buds upon the girth growth made
by the young tree in the nursery(28). Similarly the Leeds observations,
directed specifically to this point, and carried out particularly by
Messrs Prince and Cockerham, have so far failed to produce a single
case of cambial activity which is independent of the growth activity
of a bud, with the exception of the cambial activity in the neighbour-
hood of a wound, as in the case of cuttings, especially internodal
cuttings (Sledge(80)), and disbudded or ringed shoots.

The evidence, therefore, is very clear that *under normal* con-
ditions in the Dicotyledon, cambial activity begins, in the spring, in
the developing buds and spreads from thence basipetally down the
axis. Up till now no perfectly definite case is on record in which
cambial activity has been seen in the main axis and has been followed
upwards and shown to be independent of the presence of growing
buds. It must be remembered that, in such an example as is cited by
R. Hartig, the spring sun that he thinks of as warming the cambium
through the bark will also be effective in stirring any lateral buds in
the trunk into growth, and that such lateral buds are likely to be
present in a tree which is growing in a well-lighted position.

This evidence of the significance of bud growth for the commencement of cambial activity is very greatly strengthened by Jost's experimental observations upon disbudded and defoliated shoots (33, 35) etc.

In these experiments defoliation made relatively little difference provided that the buds were left; disbudding before growth had started was followed by an almost complete failure of cambium activity. The type of wood formed by the cambium could be modified by defoliation. Kuhns (47) has produced double rings in one year in this manner (see also p. 345). Jost's numerous experiments with the epicotyl of *Phaseolus* also showed that cambial activity in this organ did not depend upon the presence of the cotyledons below with their food stores, but upon the normal growth of the young foliar organs above. The experiment illustrated in Fig. 1 is also very significant. The epicotyl has been split through in the median plane, at right angles to the plane running through the cotyledons, and then one of these epicotyl strands has been severed transversely. After a few days, vigorous cambial activity will now be found at *a*, whilst at *b* the cambium will show no indications of activity, although the food reserves in the cotyledon are much more accessible to *b*. Thus once again the emphasis is upon a basipetal propagation of cambial activity from a growing foliar organ above, and translated into terms of the renewal of cambial activity in a tree in the spring such evidence supports the view that in the axis of the tree the renewal of cambial activity will wait upon renewed growth activity within the buds.

Fig. 1.

By "cambial activity" in the above brief account of its recommencement in the spring in the Dicotyledon, it will be clear that tangential cell division has been meant. Nothing has been said as to whether the new cells formed then remain part of the cambium or are added to xylem or phloem. In the published statements to which reference has been made, the cambial activity described has given rise to the new spring wood, of which tissue a broad band is often formed before any lignification is visible in it (43, 44). The observations of Cockerham at Leeds (7) show that in *Acer Pseudoplatanus* the first cell divisions giving rise to new phloem also occur at an early date and progress throughout the stem from the base of the buds in the same basipetal manner.
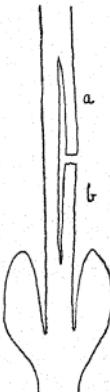
Finally, it should be pointed out that a large number of everyday experiences of the growth habit of woody perennials reinforce this conclusion that the renewal of cambial activity in such plants, under normal conditions, shows an obligate connection with the growth of the buds upon the axis. Thus, in pruning, it is axiomatic to cut the stem just above a node. If a stub of stem is left projecting above such a node, when cambial activity recommences on the pruned shoot, it will start in the bud and thence work downwards; there will be no renewal of cambial activity in the stub of internode projecting above this bud, the tissues of which will gradually wither and dry, if they do not actually decay. In the spring of 1929, in England, the hard late frosts killed off the upper shoots in many trees and shrubs. On these plants, no further radial growth has taken place on the upper parts of the twigs, and these upper shoots, devoid of living buds, are gradually dying back. On older branches small adventive buds have been forced into active growth. Beneath these buds radial growth has again occurred. In the course of time the increasing girth of these healthy shoots will displace the withered shoots of the spring of 1929, which will fall, and all traces of the damage done by this frost will thus disappear. Observations of this type will be in the recollection of every reader; on the other hand, the writer is unable to recall any case of cambial activity in woody plants in which cambial activity has initiated on a growing woody axis above the insertion of all living buds, whilst all cases known to him of cambial activity commencing or continuing independent of buds are confined to isolated pieces of stem or leaf where the activity is very short-lived unless new buds regenerate on the upper part of the isolated cambial tissue.

The initiation of cell division in the cambium in the Conifer

In the case of the Conifer, statements about the time and place of resumption of cambial activity after a rest period seem to be even more conflicting.

Our observations at Leeds have shown us quite definitely that in many Conifers cambial activity is resumed independently in the main axis and main branches, but in either case cambial activity will begin at the base of the breaking buds, from whence it will be propagated basipetally down the shoot. In the light of these observations, which will be published more fully later, the recorded observations to date seem to tell a connected story. Thus Brown[3] states that in *Pinus rigida*, at Ithaca, cambial activity, as indicated

by xylem formation, began separately in trunk and branches at some distance behind the apex and spreads from thence both upwards and downwards. In a later paper(4) he records cambial activity in *Pinus strobus* as beginning first in the upper parts of the axis. In both these papers the statements are not sufficiently precise to exclude a commencement of cambial activity in connection with buds, though they do not suggest it. Hastings(27) is inclined to trace the origin of the cambium to the zone of the branch where the oldest of the evergreen leaves are present, and to the bud in the only deciduous Conifer he studied (*Taxodium distichum*). Thus in hemlock, where the leaves persist for some seven years, he thought that cambial activity began on the surface of the seven-year-old shoots. Knudson finds in the American larch at Ithaca that radial growth begins in the middle of the trunk, though it also begins separately at the apex of the branches(41). We must remember, in connection with the North American work, that what is seen in spring may be the resumption of cambial activity at a point where it was arbitrarily stopped in the autumn by the advent of freezing temperatures, and that condition may be different where the winter is milder. Morikawa states that in Japan the extension growth of the buds of *Pinus densiflora* and *P. Thunbergii*, in trees ten to fifteen years old, begins about the end of February (mean temperature 5° C.) and that the commencement of radial thickening on the upper part of the two-year-old shoot begins at about the same time(61).

Resort to experiment also gives results which are in accordance with this separate activity of cambium beneath the bud and upon the older axis. Thus whilst Lutz(53) found that a defoliated and disbudded *Pinus* kept quite healthy until December, but showed no radial growth, the behaviour of some cut-down stumps reported by Th. Hartig(23, 24) shows that some Conifers can continue cambium activity in the entire absence of leaves and buds. Pine and spruce fail to do this although, if food reserves were the only requirement, these trees frequently show root unions with other trees of the same species, so that food should on some occasions be available. On the other hand, the stumps of larch and white fir can increase in girth for years. This may be due to root unions, but Th. Hartig found a larch stump alive and active for twelve years in the centre of a beech-wood, with no other larch near. On the other hand, a disbudded and defoliated twig does not grow. Hartig concluded that the radial growth of the stumps of larch and fir was due to the food reserves stored in them; in the pine stump these reserves are generally trans-

formed into resins. Some defoliation experiments of Th. Hartig, without disbudding, show how closely correlated cambial activity is in these plants with food reserves. In a pine, defoliated in spring, an annual ring of half the average breadth was formed that year; in a larch similarly treated the ring was the normal size. In the next year the ring was reduced in both plants to a few tracheids, in the following years it increased in proportion to the increasing foliage, so that the ring was back to normal proportions, in the larch, after six years, in the pine after twenty years. Hartig concludes there are more food reserves in the larch.

On another occasion a number of 25 ft. Weymouth pines were defoliated in February. The new growth of the apical shoots is perfectly normal, food reserves may even accumulate in them; behind this a quarter to a third of the normal breadth of the new ring is present, formed at the expense of the bulk of the food reserves in the stem. Next year there is present about eight times as much foliage and new shoot growth, and the young shoots have about a quarter to a third of the usual amount of radial thickening, but downwards this radial growth falls off very rapidly, and from the five-year wood downwards there is no new radial growth at all. The starch reserves are also gone, practically completely from the new shoots and quite completely from the old wood.

The short shoots with the bifoliar spurs are also very interesting in connection with radial growth. They may bear two pine needles for five or six years but, after the first year, no new tracheids are formed though the phloem still increases in amount. If the bifoliar spur is stimulated into renewed extension growth as the result of cutting off the apical bud, then radial growth commences again. The leaves of most Conifers complete their growth in length in the first year, though Kraus[45] describes *Pinus* as an exception, but Frank found that the bundle in most Conifer leaves still increased in girth, and whilst the xylem increased very little, or not at all, the phloem might be increased from six to about twenty or more elements. In the radial series, in the phloem, in *Taxus* leaf for instance, three or four elements were added each year up to the fifth[15]. With *Pinus Laricio*, Jost tried the experiment of disbudding, leaving the leaves on, the disbudding being carried out on March 3rd. Some secondary growth was obtained, but the wood was of an abnormal type, mainly parenchyma filled with contents, with occasional deformed tracheids scattered amongst it. Jost was able to conclude from a series of such experiments that the end bud was of great importance for cambial

activity, the leaves being of very little significance. MacDougal notes that, with *Pinus radiata* in California, the removal of the leaves early in the growing season has more effect in reducing radial growth than the removal of larger leaves a little later (55).

These data are difficult to summarise; they show that normal apical growth is very essential for normal radial growth, but they suggest that cambial activity may start quite independently of the buds, and in some large tree stumps, free from adventitious buds, it may continue for a considerable period. In the normal tree these observations must be regarded as leaving open the question of the degree of connection between bud growth and cambial activity. Cambial activity, as distinct from xylem differentiation, is very dependent upon the food supply; as a result the amount of radial growth may be profoundly modified by defoliation. Cambial activity may continue, apart from xylem differentiation, as in the leaf and the bifoliar spur, and to some extent in disbudding without defoliation.

The discussion of these somewhat conflicting data may be postponed for the moment. In retrospect, it would seem that the significance of renewed growth in the bud to the initiation of cell division in the cambium on the face of the wood of the previous year is much better established for the Dicotyledon than for the Conifer, and that no clear exceptions apart from wound phenomena have so far been recorded. This is of interest because the discussion of the differentiation of the xylem in the hard-wood tree in the previous paper (67) suggested that for this process to take place normally a local resumption of cambial activity was necessary, which should progress forwards from one region of the tree over the rest of the axis. Apart from wounds there are as yet no clear cases of cambial activity in the Dicotyledon which do not comply with this condition and wound wood is often peculiar in the Dicotyledon in structure, in particular it consists of a mass of square-ended tracheids, vessel segments and lignified parenchyma, or at least it usually contains no elongated fibres (Sledge (80)).

If a herbaceous stem is examined, in which vessels are restricted to local regions in the vascular ring as in *Lysimachia vulgaris* or in *Coleus*, pointed elongated fibres will only be found in the xylem in the neighbourhood of the vessels. These fibres, then, may be the result of the expansion in girth undergone by the vessel elements. The latter, again, will be found to be associated with the leaf trace and so, in the hard-wood or broad-leafed tree, leaf production, vessel

differentiation and fibre production are all found to be closely linked phenomena. We have seen already that they are all associated in the process of symplastic deformation of the fibre initials which is associated with the basipetal progress of cambial activity and vessel differentiation in these woody plants (67). In a later paper in this series we shall see that these processes are also connected with the delivery of water and solutes to the growing shoot when elongation growth is resumed in the bud in spring.

In the Conifer, although connection between cambial activity and bud growth is often close, the evidence suggests, though it does not prove, that the connection is less obligate. This is the more interesting because the process of xylem differentiation in this type of cambial activity is not dependent upon any gradual displacement of the process of xylem formation and differentiation along the axis of the tree, nor is the differentiation of the leaf associated with vessel and fibre production in the foliar trace.

THE MAINTENANCE OF CAMBIAL ACTIVITY

The basipetal spread of cambial activity

Until the connection of cambial activity in the trunk with the buds of small lateral members which may lie close to the trunk has been more closely investigated, it will be impossible to say whether cambial activity actually spreads downwards more rapidly in a tree in which the trunk is more exposed to the sun. Where the process has been closely followed, attention being paid to the activity moving down from lateral branches, it is striking to notice how slow this basipetal movement of cambial activity may sometimes be. Thus, in the bush type of apple trees, Swarbrick noted that up to the middle of July the amount of new xylem formed was greatest in the one-year-old shoots, whilst in a standard plum tree, cut down on June 15th, 1926, no vessels had been formed in the trunk at 18 in. above the ground, although several rows of vessels were present in the one-year-old shoots (83). On both Dicotyledons and Gymnosperms cambial activity begins in the shoot before the root and in the main root before the subsidiary branches. Von Mohl found the cambium to be some weeks later in commencing activity in the roots than in the twigs, and Gulbe found it some five weeks later in the main root than in the one-year shoots (17). In many cases every annual increment of growth finding its way basipetally down the trunk does not appear to register its presence in some part of the root system. This

point is a very difficult one because, as a rule, the root system is a complicated system of "scaffold" branches from which annual crops of young roots spring and which themselves are of uncertain age and with anatomical connections to the parent axis which are very obscure. Similarly, Th. Hartig's observations on defoliated trees show that the food supplies of the new crop of foliage at the tip of the tree are unable to support a cambial activity which can be propagated so far as the base even of the stem, and the usual idea of the forester seems to be that in close-growing, high-forestry conditions, cambial activity may already be failing in amount before the basipetal wave of renewed activity has even reached the base of the trunk. In the older tree, a position of maximum vigour of cambial activity on the trunk may thus be determined, and with increasing age and with leaf-bearing branches still further removed from the base, this zone of maximum vigour moves further up the trunk in the way in which, as previously described, Sanio noted in the Conifer that the position where the tracheids were of maximum length was to be found higher up the tree in rings of increasing age (66).

Where several branches join a main stem, an impetus to cambial activity below this point of union may come downwards from any, or all, of these branches to affect the cambium of the axis below. The extent to which such impulses to activity can be integrated, to what extent they depend upon time of arrival, to what extent upon the movement of supplies downwards, etc., are complicated problems. These same problems have been considered of recent years, but from a very different standpoint, particularly by Huber (30) and Jaccard (31). It is hoped later to re-examine this question, which requires a close comparison of the increment of wood laid down upon the branch systems and upon the trunk at various heights.

At least, however, it may be pointed out that the *time* at which cambial activity begins is one important factor involved and, as R. Hartig and Th. Hartig have, in particular, emphasised, the relatively small increment of wood usually added in the root may be due to a relatively late start of cambial activity in wood formation, which may not be accompanied by an equivalently late finish.

Extension growth and radial growth

Although in Conifers there may be a separate commencement of cambial activity in the main axis, in both Conifers and Dicotyledons the revival of cambial activity in the young shoots is certainly closely associated with the outgrowth of the bud. This fact is of

fundamental importance, and will form the basis of a re-examination of water movement in the tree in another paper in this series. We have already seen(65) that xylem differentiation in the procambial strand, which traverses the developing internode and runs into the foliar primordium, creates an osmotic system, separate from the main xylem system of the plant, which to a large extent controls the flow of sap and solutes to the meristem and the vacuolating dividing cells of the shoot. Now again we are confronted with a more or less isolated xylem system, developing in thin tongues of new tissue differentiating down the surface of the wood beneath each bud and then drawing upon the water store piled up in the main trunk and branches of the tree during the winter months.

Thus a movement of sap takes place along these newly differentiating tracheal elements which drives from the surface of the old wood *into the buds*. The movement of water and solutes in the tree thus appears in a fresh light, and at the same time we find extension growth in the new shoots intimately related to the cambial activity proceeding on the surface of the old wood beneath them. It now becomes clear why Schellenberg finds a close correlation between the amount of vessel formation in the wood of these shoots and the vigour of longitudinal growth they exhibit(75). In the differentiation of these new osmotic systems sugar will be released within them and will be carried forwards with the movement of the sap into the growing region of the shoot. The more vigorous the vessel differentiation, the greater the amount of sugar released to flow forward into the shoot apex, and the greater therefore the quantity of sugar subsequently found in the growing region of the shoot.

Usually this spring extension growth is of relatively short duration, and in England the new crop of leaves are fully exposed on the trees and extension growth has often ceased, at least for a time, in June. Similarly the early tangential divisions of the cambium, which give rise to a broad band of tissue that rapidly differentiates into xylem, often takes place with great rapidity. During this stage of cambial activity new cell formation has outstripped differentiation and by the early weeks in June frequently a very great part of the xylem of the larger branches has been formed. Throughout this xylem vessels are differentiated and the wood has the characters of spring wood.

Then with the accumulation of carbohydrates in the new shoots as the result of photosynthetic activity with little extension growth, the cells released to the inner side of the cambium are seen to be

behaving differently. In ring-porous woods few, if any, vessels are now differentiated and, in diffuse porous woods, vessels differentiate more slowly and less frequently.

At the same time, the wood walls thicken considerably, at the expense of the extra supplies of carbohydrates that are now moving downwards from the leaves and are not being utilised in much extension growth. Thus, wood of the characteristic type described as summer wood is being formed(1). In the ring-porous species Lodewick finds that the inception of summer wood synchronises with the final stages of leaf extension(52). In the white ash in America in particular, but in other ring-porous species also, he finds a definite tendency for the formation of the spring wood to be completed throughout the bole before summer wood can be seen to appear at any point. These ring-porous types show the commencement of cambial activity coincident with the first breaking of the buds, so that further work may show that, in this type, extension growth of the buds and the vessel formation of the spring wood are very closely connected.

In trees in general the periods of cambial activity and of extension growth do not show close correlation, though certainly the great burst of activity associated with spring wood formation seems to be causally related to the vigorous shoot growth of the same period.

Von Mohl(50) made measurements of the radial growth in different seasons which are given, in the following table, as an average daily increase in millimetres for the period between two observations.

TABLE I.

(*From von Mohl.*)

	Gymnocladus canadensis	Gleditschia macracantha	Tilia argentea	Populus graeca	Pavia lutea	Morus alba
May 2nd–30th	0·078	0·114	0·208	0·23	0·143	0·0
May 30th–June 22nd	0·09	0·254	0·6	0·48	0·35	0·1
June 22nd–Aug. 2nd	0·22	0·355		0·437	0·38	0·25
Aug. 2nd–31st	0·23	0·2	0·4	0·24	0·03	0·6
Aug. 31st–Sept. 30th	0·08	0·0	0·16	0·0	0·0	0·24

Of these trees, *Morus* grew in length right up to the end of the period, until the shoots were frozen at the tips one night: *Populus* and *Pavia* both form terminal buds; in *Pavia* this was showing by June 22nd with terminal growth already finished, in *Populus* growth stopped at the end of August. The remaining three trees throw off

the tops of the growing shoots. In *Gleditschia* and *Gymnocladus* abscission took place about the end of July or beginning of August, in *Tilia* the time of abscission was not observed. In three of these trees radial growth continues long after growth in length has ceased (*Gymnocladus*, *Gleditschia* and *Pavia*); in no case has radial growth clearly ceased before growth in length. Similarly, Jost points out that cambial growth may continue longer in autumn in such trees as beech and oak, where only a limited amount of foliage already laid down in the bud develops during the season, than in trees where new leaves continue to be laid down at the growing point and developed for a somewhat indefinite period during the same season(34).

The development of foliage on the axis, as is shown by the relative length of the internodes along the one-year-shoot, usually increases in vigour up to an optimum period somewhere in the season and then falls to the end of the season. Occasionally there is more than one period of relatively vigorous growth in the same season; thus Tammes has described two sets of long internodes, separated by a group of comparatively short ones as a frequent occurrence, especially amongst bush plants(85). She has also observed the same thing in cases where the "Johannistriebe" have grown. These may be separated from the growth of the original shoot by a period of complete cessation of ex tension growth; in this case Jost has seen a separate annual ring as the result of their development, so that two rings are present in the one-year-shoot(35). The second ring usually dies out a short distance down the shoot. This appearance of two rings, which were very distinct in some cases, might mean that radial growth had also ceased before the formation of the "Johannistriebe," but the change in the type of the wood would produce the ring without a complete stoppage of growth necessarily taking place.

Temporary cessations of radial growth have been recorded by various observers. Lodewick recorded two rest periods at a point breast high in the trunk in *Fraxinus Americana*, one for about ten days after June 9th, the other between July 16th–27th. Incidentally Lodewick had a dendrograph record of radial increase also, and notes a considerable discrepancy between the increase in girth recorded by this instrument and the data obtained from histology(51). Brown records two optimal growth periods for radial growth in *Pinus strobus*, one in the spring which he associates with the utilisation of the stored food in the trunk, the other in July and August, during which he assumes that the photosynthetic products of the season are being utilised(3). Mischke(58) noted two similar optima in *Pinus*,

but sought to correlate them with special rainfall conditions during the period in which his material was collected.

Jost[34], in a series of measurements of growth increment made every few days on a number of species, noted two optimal periods of radial growth in all but three species examined. Maximal growth occurred at very different times in different species, although growing under similar climatic and soil conditions. He concludes that this method of radial growth is characteristic of the species, but that it shows no obvious correlation with that other cyclic process-leaf production. As Jost has traced so very clearly the relation of leaf development to the recommencement of cambial activity, this lack of correlation between continued cambial activity and leaf development is not likely to have been accepted without close scrutiny.

The annual ring

Undoubtedly this periodicity of growth is connected with the periodic change in the type of wood formed, the well-known transition from spring to summer or autumn wood. The spring wood has the wide lumen and thin wall which is associated with rapid extension, when water supplies are perhaps more plentiful than carbohydrates: the thick walls of the summer wood suggest a slower extension when carbohydrate supplies are more accessible. This is supported by André's work on the effect of nutrition upon the wood of *Nicotiana*[1]; thinner walls are obtained when the carbohydrate supplies are cut down either by ringing, defoliation or shading.

Von Mohl points out that the appearance of the annual ring in the Dicotyledons and Gymnosperms respectively seems to be due to a different cause[59, 60]. In the Dicotyledon, from year to year the difference in the ring is mainly due to a varying amount of thick-walled summer wood; in the Gymnosperm the variable factor appears to be the depth of the zone of thin-walled spring tracheids. If the Conifer is restricted in development by a poor soil, the result is less spring wood and a very solid wood, whilst the Dicotyledon under the same conditions produces less summer wood and therefore a more spongy timber, if grown under such unfavourable conditions. This difference in habit is very suggestive when it is remembered that the spring wood of the Dicotyledon is associated with shoot extension, and that the relation of shoot growth to radial growth seems much more obligate in this type than in the Conifer, so that every year that extension growth is made in the Dicotyledon the spring wood must be laid down.

The same rules do not seem to apply to the formation of secondary xylem in roots; thus, von Mohl found that in *Abies pectinata* the more vigorous the growth and the wider the ring in the root, the wider, even up to one-half the total diameter, the zone of thick compressed elements formed. In *Fraxinus excelsior*, on the other hand, the darker thick-walled elements of the stem rings were not represented in the annual rings of the root, and in the outer part of a symmetrically built root the rings were all so porous that it was quite impossible to discern their limits. At the same time, in *Fraxinus*, though so many tracheae were present in the ring, the individual vessels were smaller in diameter than in the stem. Another curious difference between the tracheae of stem and root in *Fraxinus* is the frequent presence of thyloses in them in the stem in all but the first-year wood, whilst thyloses are very rare throughout the xylem of the root.

According to Th. Hartig and von Mohl, the relatively narrow rings of wood in the root are readily explained because, as already seen, cambial activity often begins several weeks earlier in the stem than in the root. Hartig finds that sometimes as a result cambial activity may be restricted to a period of two months in the root. In many cases this reason would not seem very convincing, as the cambium may be as late in stopping growth in the root as it was in commencing, though Russow and Strasburger agree in concluding that von Mohl was dealing with an abnormality when he reported growth in the root as active all the winter. The later period over which the cambium activity extends, which may include most unfavourable seasonal conditions, may be partly accountable, but in most cases the very different extent of its activity can only mean a slower rate of growth during the period in which it is active. It also shows a different type of activity, the xylem thus formed has a totally different appearance, and this difference is probably connected with the conditions of growth in the root.

Cockerham[7] finds that in *Acer pseudo-platanus* the distal, thin region of the root, which retains the same diameter for very long distances, shows an almost uninterrupted but very slow radial growth. Upon this continuous activity, in the proximal root region, is superimposed the basipetal impetus to more vigorous radial growth which reaches the root from the trunk and which lasts for a relatively short period. This basipetal wave of radial growth activity is presumably responsible for the greater girth of the roots near the trunk, a girth which tapers fairly rapidly into the long uniform whip-like

roots, in which Cockerham has observed this slow, continuous characteristic "root cambial activity."

Brown states that in *Pinus strobus*, near the trunk, where the roots are freely exposed to air, the radial growth of the root is exactly similar in nature and extent to that of the stem, and where the main roots are in the light and air, whilst their bark becomes more broken and porous, this stem-like type of radial growth is generally found (4). It is natural, therefore, to connect the difference in the types of cambial activity and xylem differentiation with the lesser degree of aeration of these tissues in the root. Growing frequently in watercharged soil, with few if any lenticels or other breaks[1] in the cork, which is of pericyclic origin, these tissues have less communication with the outside air, especially in the younger roots. Under these conditions growth is slower, the wood less lignified, more full of water and freer from air, a condition which probably explains the absence of thyloses. In the stem of *Fraxinus*, thyloses are similarly absent from the first-year wood, which during that year is similarly full of water and free from air, but in later years, when the wood during the season is apt to be charged with saturated air, the tracheae are full of thyloses (Klein (38)).

Radial growth of the phloem

There are comparatively few observations as to the behaviour of the phloem during the season—the question is obviously of importance and more data are urgently required. Swarbrick has described its early swelling in the spring in the apple. Brown gives the date March 29th for the same phenomenon in *Pinus strobus* at Ithaca. This phenomenon, which suggests the intake of water, may be connected with the disappearance of starch and temporary accumulation of sugar which is reported for this same tissue, but on the whole for an earlier date, between the middle of January and the end of February. This swelling, in Swarbrick's observations, was definitely dissociated from cell division, and usually the first divisions in the phloem are put much later; the only exception seems to be the statement of Knudson about the American larch in which he saw the cambium active first in forming phloem in the spring. Cockerham finds similarly in *Acer pseudo-platanus* at Leeds that the cell divisions separate new phloem elements upon the outer face of the cambium some weeks earlier than new xylem elements are formed to the inside. This early activity in phloem production also begins at the buds and

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[1] In *Pinus*, of course, no lenticels are present in the cork in any case.

works from thence basipetally down the axis. Lodewick, who noted in *Fraxinus Americana* xylem formation commencing as the buds opened, found the first phloem elements were formed several weeks later, and continued to form until defoliation in autumn. Strasburger and Russow both found phloem formation commenced later than that of the xylem, but continued much later. In fact, they state that the developing stages of the sieve tubes are to be found in the winter rather than in the summer, when the first phloem element outside the cambium cell will usually be found to be fully differentiated. Only in *Juniperus communis* and the main axis of *Taxus baccata* amongst Gymnosperms were cambium initials found to cease activity on the phloem side during the winter, and in the twigs of *Taxus* and in *Juniperus chinensis* the usual gradations were found in the winter from the cambium cell to the mature sieve tube. Strasburger similarly reports that in the Dicotyledon the stages from cambium cell to the adult sieve tube are to be found in the winter. These observations at least make it obvious that the differentiation of the phloem continues very much later than in the case of the xylem. As isolated observations suggest that it also takes place in the tree from the first-year shoot downwards, the significance of this process in connection with the downward movement of the products of leaf metabolism needs little underlining. In many trees the earlier phloem elements are clearly empty and take no part in the translocation of this food material. In such cases the differentiation of phloem elements, charged with contents, is a clear indication of downward movement of food supplies. If the time of this differentiation can be taken as an indication of the time when these food supplies reach the trunk and roots, then frequently these supplies are very late in reaching the roots. This conclusion would agree very well with the results of the analyses of Ramann and Bauer (70), which show the gain in dry weight of the roots in beech and ash as very marked between July and September, but in most trees between September and November.

This downward differentiation of the phloem will be more fully considered in a later paper. It must suffice now to point out that it shows an interesting correlation with a late seasonal growth activity which seems often to be observed in the roots of trees.

We have already seen that there is a slow winter activity of these roots in milder climates which is associated with the gradual rise of the water table in the wood of the tree throughout the winter. In the spring this is followed by a vigorous burst of root production,

long before any meristematic activity directly connected with the buds could possibly take place. This root production is of the "fibre" type, fine thin white roots appearing on all the old "scaffold" roots; in many root systems such new roots appear in bunches of fine threads at the regions where former branch roots have died down. This type of root production must bring about a very great increase in the absorptive surface of the root system (76) in a very short time. During the summer, root growth often seems to be at a standstill for some time, and during this time the gradual suberisation of exo-dermal and endodermal surfaces in the new crop of white roots may considerably reduce the absorbing surface of the root system (77). In the late summer or early autumn, about the time that this impetus to increase the radial increment of phloem is reaching the root system, a new burst of root activity is often recorded (18), and Petersen has pointed out that this new root production often syn-chronises with a fall in the activity of radial growth, as noted by xylem production, whilst on the other hand, the quiescent period for root extension, about July, correlates with a period of maximum radial growth in the older roots (62). The new branch roots formed as xylem formation ceases and phloem formation continues in the roots are often different in type to the thin fibrous roots of the spring, being thicker roots which may ultimately be added to the scaffold root system. A similar difference in the seasonal type of root pro-duced has also been noted by Mann and Ball in strawberry (54); van der Lek has drawn attention to a similar difference in the type of roots produced upon hard-wood cuttings (87).

It will be noted that the thick, relatively unbranched roots are formed in the autumn, when presumably food supplies are reaching the root system in considerable quantity. In van der Lek's experi-ments this type of root was produced when the bud on the short stem cutting only developed late. Sledge's work has shown (80) that this root has probably developed when cambial activity has started at the base of the cutting independently of the bud; in this case all the food supplies of the cutting will at first be available for the root; when the bud starts growth earlier a considerable amount of the limited food supply available must go to nourish this bud—in this case fibrous roots are formed at the base of the cutting.

THE CESSATION OF CAMBIAL ACTIVITY

The cessation of extension growth of the shoot in the summer takes place frequently when the foliar expansion is at a maximum

and conditions are optimal for photosynthesis. At the same time these are, of course, the conditions for the greatest transpiration, which in the long summer day predominates over root absorption, so that the water table is falling in the xylem. The adult leaf, with the high osmotic pressure of the leaf cells, from which evaporation is constantly withdrawing water, may still be able to withdraw water by the tension exerted on the water columns of the first-year wood in which no air is yet present. Under these conditions the separate vascular systems associated with the origin of new foliar initials cease to develop, and growth in length comes to a standstill, although meristematic cells may still continue a limited amount of activity in the buds.

This cessation of growth in length at a time when photosynthetic activity is at a maximum is followed by an accumulation of food reserves in the shoot, which first reaches "saturation point" at the apex beneath the developing bud, and spreads from thence gradually down the shoot. In the older parts of the stem the starch appears first in the inner rings of xylem, and its appearance near the cambium ring seems to be an indication that cambial growth has also stopped. Cambial growth frequently continues for a long time after shoot extension growth has stopped. Swarbrick's observations on the apple show that it stops in this plant first in the shoot of the current year, and that further down the axis it remains active progressively longer. Activity in this case is judged by the continued formation of new xylem elements, and there is a general agreement that this form of cambial activity persists longer in the root than in the main axis above ground. With further observations probably Swarbrick's conclusions will prove to have a very general validity and cambial activity will be found to cease as it began, first in the young shoot, and from thence the cessation of activity will be found to extend to lower and lower regions on the axis. Lodewick's recent observations are in good agreement (52).

The reason of this cessation of activity is still a matter of speculation. Proebsting's analyses of defoliated shoots of apple do not support the suggestion that the cessation of radial growth in this case has been brought about by lack of food (69). The content of such defoliated twigs in sugar is little different from the normal. Similarly Jost noticed in many of his experiments that when radial growth had been inhibited as the result of interference with a foliar organ above this region of the axis, the tissues in the region where radial growth failed to occur were often very full of starch. On the other

hand, such defoliation experiments as Th. Hartig carried out with Weymouth pine showed a very close correlation between the amount of radial growth and the food reserves available. Whilst radial growth may continue in the region of the shoot where the new foliage provides some nutriment, lower down the axis, as soon as the reserves in the stem are exhausted, no further radial growth takes place till, with increasing foliage in subsequent years, the reserves are replenished. The same absence of radial growth towards the base of the trunk was noted by Harper in larch which had been defoliated by an attack of the larvae of the sawfly, *Nematus Erichsoni* (19), and by Bailey in pine in the years following serious defoliation by the budworm, *Cacaecia fumiferona* (2). On the other hand, the observations of Th. Hartig upon radial growth in the stumps of larch and fir show that, provided the food reserves are adequate, the formation of xylem by the cambium can continue with considerably less dependence upon the growing foliar organ above than in the Dicotyledon.

DISCUSSION

Internal factors governing seasonal cambial activity

It would appear then that radial growth in the Dicotyledon is more independent of the food reserves than it is in the Gymnosperms; on the other hand, it is more sensitive to some internal factor which is brought into play by foliar development upon the growing axis. But the growth of the foliar organ and its associated part of the axis has been seen to be completely dependent upon an adequate supply of sap which, in this case, is provided by the differentiation of the vascular system associated with this growth unit (65). The cambium, both unvacuolated fusiform initial and vacuolated ray initial, must be similarly dependent upon an adequate sap supply.

Here is a possible reason for the close correlation between foliar development and radial growth in the Dicotyledon, rather than in the Gymnosperm, because, during the summer in the former plant, air is gradually replacing water in the older wood. At the close of the season, as the air fills the intercellular spaces in the wood up to the current year's growth, the intercellular spaces in the relatively broad medullary ray permit this air to move forward in the ray till it reaches the cambium. Then at least the supply of solutes on the side of the cambium facing the xylem, so far as these are drawn from the phloem, is cut off. This state of water deficiency is likely to be reached first where the wood is nearest to the transpiring foliage. It

is therefore natural, if this is the cause of cessation of radial growth, that it should cease first in the current shoot and then subsequently in successively lower regions of the shoot. In the root, if the root contains a well-developed intercellular air system, the same factor may bring about the cessation of growth in the root system, but in the younger roots, surrounded by a continuous sheet of pericyclic cork, and with at first very little development of air spaces within the root, radial growth may continue when it once commences until the external temperature or the lack of food supplies brings it to a halt. Von Mohl has described radial growth in roots as continuing all winter in some cases.

Certainly shortage of food supplies cannot be claimed as the reason for the cessation of radial growth in the summer. An excessive accumulation of food might rather be suggested as a possible cause. But the fact that, with a wet and warm summer, both longitudinal growth and radial growth may be restarted, adds support to the view that the governing factor is rather a lack of moisture. For the present the most likely hypothesis seems to be that this deficiency of water acts through the displacement of water by air in the intercellular spaces of the tissues of the cambial ring itself. The application of this standpoint to the Gymnosperm is at present a very difficult problem. Direct displacement of water by air in intercellular spaces near the cambium cannot be invoked in the present state of our knowledge. On the other hand, with transpiration in excess of the intake of water by the root, the number of tracheids in which water is disappearing, or only retained under tension, may rapidly increase, and possibly as such tracheids approach closer to the cambium the supply of sap for the maintenance of its activity becomes deficient. The behaviour of the axis of the bifoliar spur of pine, in which xylem ceases to differentiate unless sap is diverted to it as the result of the cutting off of the apical shoot, suggests that cambium activity in xylem formation here also requires a minimal supply of sap maintained in the young wood near the cambium.

During recent years, since this theory has been tentatively considered, observations have been made as occasion permits upon the distribution of air in the intercellular spaces in the region of the cambium. If sections are made of fresh twigs, whilst the cut surface is bathed in glycerine and the section immediately examined in glycerine, bubbles of air will be found to be still trapped in many of the intercellular spaces amongst the ray cells of the Dicotyledon. In summer and early winter these air spaces will be seen to be con-

tinuous and unbroken from the inner rings of wood, through the cambium out into the phloem and cortex. But when sections are taken in the spring, as cambial activity is about to recommence, a very different state of affairs reveals itself. The whole ring of wood in the immediate neighbourhood of the cambium shows itself as a translucent ring of tissue in which all intercellular spaces are free from air. This change in the distribution of air and water in the intercellular spaces of the rays in the neighbourhood of the ring may well have a causal relation to the renewal of cambial activity in the Dicotyledon. More observations will be necessary before any statement can be made about the Conifer in this connection. In the softwood tree the air spaces in the ray are much smaller, and the displacement of water by air in these small spaces does not take place so readily; thus it is quite impossible to blow air (under pressure of about two to three atmospheres) into the stem of such a tree, along the pith, and then find it escape along the rays out to the surface of the wood except through those large rays which contain resin canals.

As Sledge has recently pointed out, the causal relationship between sap in the intercellular space and the renewal of cambial activity would also explain the exceptional cases where cambial activity commences without any connection with the buds(80). Thus the intercellular spaces in the neighbourhood of a wound are always injected with sap and, therefore, cambial activity in isolated shoots or leaves, when used as cuttings, readily finds an explanation. This point is discussed more fully by the writer in conjunction with Dr C. F. Swingle, in a general discussion of problems of vegetative propagation which are closely connected with this question of cambial activity (68).

The basipetal propagation of cambial activity

Whilst the cambium seems to change into its swollen growing condition in the spring, all over the tree at about the same time, cell divisions always begin in certain places, and from thence spread gradually over the cambium on the surface of the old wood. In the Dicotyledon, apart from wounds, there is no evidence that this activity of cell division ever proceeds in any but a basipetal direction, from the buds on the shoot down branches and main trunks and then out along the roots to the youngest branches. Further evidence as to cambial activity in roots, however, is required. In the Conifer there may be evidence of a cambial activity in the trunk which is separated from the basipetal propagation of cell divisions from the

buds down the branches, but there is as yet no real evidence of any *upward* propagation of the cambial activity in the trunk.

The method of xylem differentiation in the Dicotyledon, described in the previous paper, seems closely correlated with such a gradual spread of its growth activity, and with the similar basipetal spread of the cessation of its activity which has also been noted. It is not clear, at present, however, why this spread of activity in cell division is so universally downward, though the fact elucidates completely the peculiarities of radial growth in inverted cuttings and in inverted grafts. Another basipetal tendency in the axis is shown in the downward movement of organic solutes in all parts of the axis except the first-year shoot, which is associated, probably, with the downward differentiation of the phloem and with the downward transport of substances through the phloem. Plett's observations upon internodal cuttings (63), confirmed in the Leeds laboratories, (68, 80) show that, even in such small isolated pieces of stem, there is still a tendency for a downward transference of the food material, starch often disappearing from the parenchyma at the distal end of such a cutting, whilst it is retained or even still accumulates for a time at the proximal end. This tendency to downward transference of substances through the phloem is by no means clear, and will be submitted to further examination later. It may possibly be associated with the basipetal propagation of cell division in the cambium, which lies just upon the inner surface of the most recently differentiated phloem. Certain evidence from experiments upon vegetative propagation, which has been presented elsewhere (68), points in this direction, and cambium activity always seems to be closely connected with the phloem. Thus in the transitional region, in the hypocotyl, where the relative positions of xylem and phloem are changing, Chauveaud's figures (6) show the cambium much more closely associated with the phloem than with the xylem.

In concluding this brief examination of our knowledge of the seasonal activity of the cambium, it is perhaps permissible to emphasise the great significance of the results that emerge, particularly as such results might so readily be extended and corrected if the attention of a small army of observers, spread over many countries, were only directed to the relatively simple points at issue.

The activity of this intercalary meristem has proved to be linked in the most unmistakable manner with the activities of the apical meristem. Usually the impulse to its initiation in the spring derives from the shoot apex above, whilst its waning activities at the end of

the summer show a suggestive correlation with a final burst of activity upon the part of the root meristem.

At the same time the correlated growth changes concerned make a most suggestive picture in connection with the water movements involved in the extension growth of the shoots in the spring, and with the subsequent movement of organic materials from these shoots downwards into the tree, with their storage in the axis or their subsequent utilisation in the growth activities of the roots. It will be the task of later papers in this series to follow up these lines of enquiry.

SUMMARY

The meristematic activity of the tree shows a rhythm which, whilst modifiable by external circumstances, is probably autogenic, and the result of the fluctuation in the internal factors correlating growth, including a fluctuating balance of metabolic activities.

The cambium, as an intercalary meristem, shows such fluctuations in activity which, as might be expected, are closely correlated with the fluctuations in apical meristematic activity illustrated by flower and foliar primordia production, cataphyll and foliage leaf production, etc. In mild European climates, root extension growth continues during the winter, with intake of water and a rising water table in the wood of the tree. In the spring, apparently at about the same time, throughout the tree, the cambium changes from a granular "gel" condition to a swollen, semi-fluid "sol" condition. Some time later cell division commences. In the Dicotyledon, so far as present evidence permits a conclusion, these invariably commence in the buds, and from there work basipetally downwards in the cambium on the surface of the old wood, down branches, main axis, main roots and so out to the younger roots in which, however, a certain slow cambial activity may persist most of the season. As a result, cell division may be weeks later in commencing in the trunk than in the branches, and weeks later still in the roots than in the trunk.

In the Conifer, cell division in the cambium of the young branches seems to work downwards from the buds, but there is evidence of a separate start of cambial activity in the main trunk and main branches.

The first rapid production of spring wood is closely connected with the extension growth of the new shoots; this connection is in all probability causal in the Dicotyledon, in view of the close connection between the new osmotic systems thus established and the transfer of water from the old wood into the new shoot growth.

But the maintenance of cambial activity throughout the summer shows no close connection with extension growth; radial growth usually continues much longer than extension growth. When extension growth ceases and foliar expansion is completed or at a maximum, the products of photosynthesis accumulate and a water deficit develops in the wood.

The downward transfer of the metabolic products of photosynthesis probably synchronises with the development of the summer type of wood. In Dicotyledons vigorous vegetative growth means more summer wood. The amount of spring wood formed varies but little; its constant formation is probably associated with the extension growth of the shoots which must take place every year. In the Conifer vigorous growth means a greater formation of spring wood so that relatively tougher timber is produced when the trees have grown under unfavourable conditions.

As the water deficit increases in the trunk cambial activity ceases, first in the twigs, and then basipetally downwards. This cessation is accompanied by starch storage in the wood, etc., but is probably not caused by this but by the water deficit, so that a wet summer may produce renewed extension growth ("Johannistriebe") and a fresh ring of "spring" wood, so that for a certain distance down the stem a double "annual" ring may be formed.

It is suggested that, as a result of the fall in the water content of the wood, the water in the relatively large and numerous air spaces in the rays of the Dicotyledon is gradually displaced by air, and that when this process takes place in the region of the cambium, cambial growth ceases.

Conversely, when the water table rises in the spring, the air in the intercellular spaces in the rays is displaced by water once more and growth recommences. This would explain the commencement of cambial activity in the neighbourhood of a wound, as the parenchyma cells near the cut surface would release sap to inject the intercellular spaces.

In the Conifer the intercellular spaces in the rays are smaller and the displacement of air by water less readily brought about. In these trees, therefore, cambial activity may be more independent of fluctuations in the water supply. It seems very often, however, to be affected by water supply, and in many cases it shows marked correlation with the local accumulation of food reserves.

The basipetal transmission of cell division in the cambium may be associated with the downward transfer of organic substances through the phloem.

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NOTES ON VEGETATIVE REPRODUCTION IN TWO MOSSES FROM MUSSOORIE(13)

By T. C. N. SINGH

(With 9 figures in the text)

VEGETATIVE reproduction is such a common phenomenon amongst the mosses that Professor Goebel has expressed the opinion that "almost every living cell of a moss can grow out into protonema and many produce gemmae of different kinds"(5). In most of the north-western Himalayan mosses and liverworts, vegetative reproduction has become such a fixed and rapid mode of propagation that in certain cases it has more or less eclipsed fructification(6,7). The validity of this statement would gain more confirmation by the test of research in this direction for which there is such a vast and ample field among the Indian mosses and liverworts.

The two mosses which have furnished data and facts for the present paper were collected by Professor B. Sahni in October of 1925 at Mussoorie (India), and were kindly placed at my disposal for investigation. This work was carried out during the session 1926–1927, at the Botany Department of the Lucknow University.

It is interesting to note that these two mosses (namely *Philonotis Turneriana* Mitt. and *Bryum hemisphaericarpum* C. Mull.), although growing in the same locality under similar conditions, vegetate differently. This we shall see presently when individual considerations are taken up.

Philonotis Turneriana Mitt.

Only a few cases of vegetative reproduction seem to have been reported for the genus *Philonotis*. In *P. Ithyphylla*(1) the male inflorescence near the female is gemmiferous. Reproduction by *Brut-knospe* in certain species of *Philonotis* described by Correns(2) is quite different from what I find in *P. Turneriana*. Möller(9), in a recent paper, has given a systematic study of eight species of *Philonotis* but without any mention of vegetative reproduction in them. The only reference regarding *P. Turneriana*, as far as known to me, has been made by Dozy and Molkenboer(3), Paris(11) and Engler-Prantl(4); but none of these authors say anything about its vegetative reproduction.

P. Turneriana Mitt. commonly grows quite wild in the north-western Himalayas. It is a small moss about three-quarters of an inch tall when mature, and is branched from the base round a central female shoot. The most characteristic external feature about this moss is that the tips of almost all the branches, except the central female which invariably bears the sporophyte, look lighter green than the rest of the leafy portion of the shoots. Such tips when crushed between the two fingers give a powdery touch. At the time of collection, this gave the suspicion of the presence of minute gemmae at the tips. In order to verify this point, crushed preparations of the tips were made in glycerine and also serial microtome sections ($6\,\mu$) cut and stained in gentian violet, and safranin and haematoxylin.

The microscopic examination, however, has failed to show the presence of gemmae, but, instead, a large number of bulbils (Fig. 2) are found clustered together round the growing apex (Fig. 1). These bulbils usually occur in the axils of leaves. They are attached to the stem axis by a fragile connection of tissue (which attains a brown coloration (Fig. 2, shaded portion) when the bulbils are mature), such that while mounting the entire tips in glycerine the bulbils were disjointed apart even by the slightest pressure of the cover glass. About half-a-dozen tiny leaves are present on each of the bulbils. These leaves are much smaller than the ordinary vegetative ones; but on the contrary their epidermal cells are much broader with a larger number of chloroplasts (Figs. 3, 4). No rhizoids, however, have been noticed on the bulbils, even after very careful microscopic search. This perhaps may be due to the collection being made at an early stage.

<center>*Bryum hemisphaericarpum* C. Mull.</center>

Paris[10] makes a reference to this moss in *Index Bryologicus*, but talks only about its distribution in the Himalayas and Nepal. Braithwaite[1] has recorded vegetative reproduction in several species (except *hemisphaericarpum*) of the genus *Bryum*. In the present connection, however, only two of them (viz. *B. Concinnatum* Spruce and *B. atropurpureum* W. and M. (*B. biclor* Dicks.) var. *gracilentum* Tayl.) described by him are interesting. In both of these bulbiform gemmae are formed in the axils of leaves. Marshall[8] and Schimper, Bruch and Gümbel[12] have recorded in *B. erythrocarpum* gemmae clustered in the axils of leaves, but in none of them are clear details given. However, these are the only few species in which the situation somewhat approximates to that found in *B. hemisphaericarpum*.

Engler-Prantl(4) makes a reference to this moss, but without any
mention of its vegetative reproduction.

   B. hemisphaericarpum is like other species of its genus in pro-
ducing gemmae in the axils of leaves. The mature plant is about an
inch in height and is a little deflexed on one side. The gemmae are
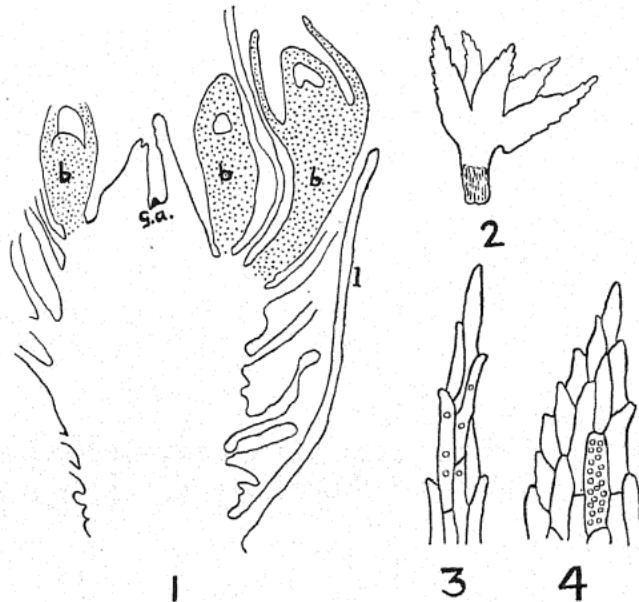
Figs. 1–4. *Philonotis Turneriana* Mitt.

Fig. 1. Longitudinal section through a lateral branch showing *g.a.* =growing
    apex; *l* =leaf; *b* =bulbil. × 193.
Fig. 2. A fully developed bulbil. The shaded portion is the tissue which be-
    comes brown at maturity. × 73.
Fig. 3. Epidermal cells of an ordinary vegetative leaf showing very few
    chloroplasts. × 333.
Fig. 4. Epidermal cells of a bulbil leaf. Unlike the ordinary vegetative leaf,
    all the cells of the bulbil leaf are packed with chloroplasts, as shown in one
    of the cells in the figure. × 333.

formed indiscriminately in the axils of most of the leaves and when
mature they (the gemmae) turn brown and are visible from the outside
through the thin translucent leaves. These gemmae are borne in such
great abundance that the plant when seen with the naked eye offers
a superficial resemblance to a mature strobilus of *Selaginella*. A some-

what similar state of affairs is also obtained in a Javanese moss(5), *Eriopus remotifolius*, which has "in the axils of its leaves numerous tufted, branched, brown protonema threads, forming peculiar two-armed gemmae at the extremities."
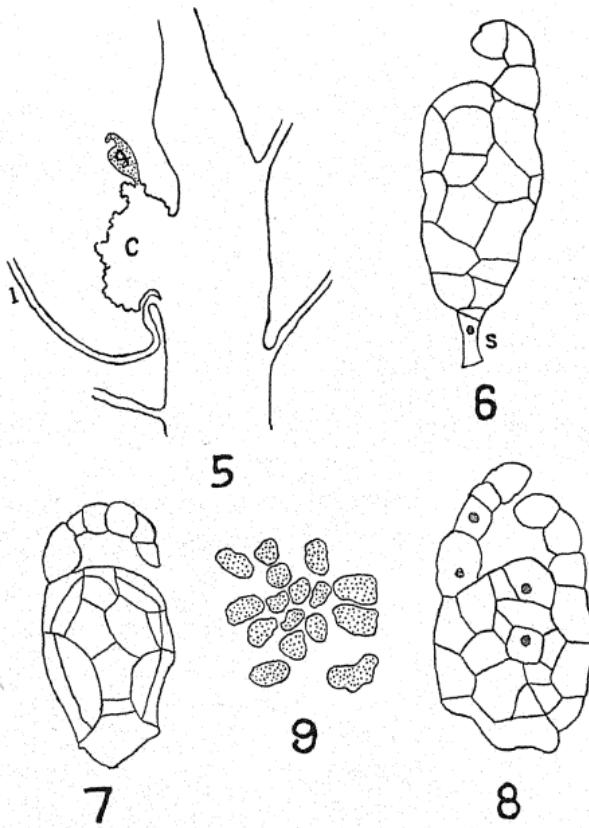
Figs. 5–9. *Bryum hemisphaericarpum* C. Mull.

Fig. 5. Longitudinal section through stem showing *g* =gemma; *l* =leaf; *c* =cushion-shaped receptacle on which the gemmae are borne. ×77.

Figs. 6–8. Gemmae in longitudinal section, *s* =stalk. ×343.

Fig. 9. Transverse section of the group of gemmae that is borne on a re-ceptacle. ×67.

A study of serial microtome sections of the plant has brought out that a thick cushion (Fig. 5) of tissue (receptacle) is situated in

the axils of leaves. On this receptacle are borne a large number of gemmae (Figs. 5, *g*, 6–8) in acropetal succession, i.e. the youngest are in the centre and the oldest towards the periphery (Fig. 9). These gemmae are multicellular and club-shaped. They are attached to the receptacle by a short stalk (Fig. 6, *s*) composed of two to three cells. About a dozen or so hooked processes are present on the apex of each (Figs. 6–8). These possibly represent the primordia which later give rise to leaves.

In conclusion it may be pointed out that a developmental study of the bulbils and the gemmae in the two mosses already described would prove very interesting.

SUMMARY

Vegetative reproduction in two mosses from Mussoorie (India), viz. *P. Turneriana* Mitt. and *B. hemisphaericarpum* C. Mull., is described.

In *P. Turneriana* leafy bulbils occur usually in the axils of leaves round the growing apex on the stem, while in *B. hemisphaericarpum* a number of multicellular club-shaped gemmae are formed on a cushion-shaped receptacle situated in the axils of leaves. The gemmae are formed on the receptacle in acropetal succession.

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IMPERIAL BOTANICAL CONFERENCE, 1930

THIS Conference was held on August 15th, 1930, at the Imperial
College of Science and Technology, South Kensington, London,
the President, Dr A. W. Hill, C.M.G., F.R.S., being in the Chair. In
addition to a number of British botanists there were present delegates
from fourteen overseas Dominions or Colonies and from four overseas
Universities or Research Institutes.

The findings of the various Sub-Committees set up by the Exe-
cutive Committee of the 1924 Imperial Conference to deal with a
series of Resolutions of that Conference were announced.

The President then invited discussion on the question of a subse-
quent Imperial Conference. Various members having expressed their
views, the following Resolution was put from the Chair:

"That an Imperial Botanical Conference take place in England
in 1935 shortly before the International Botanical Congress which is
to be held in that year in Holland."

This Resolution was carried unanimously.

The following Interim Committee was appointed: the Director of
Kew (Convener); the Keeper of Botany, Natural History Museum;
the Professors of Botany at Oxford and Cambridge; a Professor of
Botany of the University of London (to be nominated by the Chair-
man of the Board of Studies of the University); one representative
of the Colonial Office and one representative of the Dominion Office.

It was further resolved that this Committee summon a Meeting
of British botanists in the near future for the purpose of appointing
an Executive Committee for the said Conference.